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THE DEVELOPMENT OF ALPHEUS.

by

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NOTE: This paper is to be completed by a Second PART in which the special development of organs and the histogenesis of tissues from the larva to the adult will be considered.

INTRODUCTION.

The observations offered in this paper were begun in the Marine Laboratory of the Johns Hopkins University, at Beaufort, North Carolina, in the summer of 1885.

The two species of Alpheus common to the southern Atlantic coast, (A. heterochelis and A. minus), are very abundant at this point, and their eggs easily obtained, but the hardening reagents then used, (Perenyi's fluid and corrosive sublimate), proved to be quite inadequate to the purpose, and it was not until the next, and following seasons (1886&-7), while enjoying the advantages of the Marine Station at the Bahama Islands, that I was able to make a complete and satitfactory study of the life history of this animal.

Out of the dozen or more species of Alpheus common to the coral reefs and shores about Nassau, New Providence, two were selected which offered most advantages for study, namely, Alpheus praecox sp. n. (provisionally named) and another species probably also new, both of which will be figured and described in another work. The former leads a semi-parasitic life in certain sponges. It has a nearly cometely abbreviated metamorphosis, and consequently large eggs, which are favorable for embryological work.

The second species lives in the sand under loose stones, in shallow water, and hatches, like most of this genus, as an ordinary Zoëa. Its eggs are invariably light olive green in color. They are at first spherical, and measure about $1/_{40}$ of an inch in diameter. Though small, the ova of this Alpheus are quite numerous, so that it is possible, by keeping the animals alive, to obtain a pretty complete series of hardened embryos from the same individual.

The eggs of A. praecox are usually oval or oblong when laid, and vary somewhat in size and shape, and greatly in color. The average of the long and short diameters is approximately $1/_{23}$ inch. The color may be bright green, yellow, brown, etc. in individuals from the same sponge. (On these color variations see Univ. Circular No. 63.) A full account of the ~~history~~ habits of these animals is reserved for another place. Some notes on the metamorphosis, habits and development in the egg, of this and other Alphei have already been given, (Univ. Circular. No,s 54, 63.)

As the development of Alpheus has not been previously studied, except as regards the metamorphosis of the Beaufort species, there is scarcely any work of others to refer to, which bears directly upon our subject.

The literature of Arthropod embryologyis, however, very great indeed, and recently, during the progress of this work, several important papers have appeared on crustacean development. These will be referred to in another section.

Packard (9) seems to be the first to notice the shortened metamorphosis of Alpheus heterochelis, but his description of the animal when it is about to hatchis inaccurate and incomplete. In some notes published in the American Naturalist in 1881, he states that both this and the small green Alpheus (A. minus.) occur abundantly at Key West, Florida, in the excurrent orifices of large sponges, at a depth of 1 to 2 feet or more of water. This fact is interesting, and, as we have already pointed out the abbreviated development of Alpheus is correlated with a semi-parasitic mode of life.

The metamorphosis of the Beaufort Alphei was then carefully studied by Brooks, (10) and a short abstract of his results was published in 1882. So far as I can learn, this is all that has been previously done in the embryology of this form.

METHODS OF WORK.

Several prawns, as Stenopus and Pontonia, repeatedly laid eggs that were fertilized in aquaria, and no doubt I should have succeeded equally well with Alpheus, if sufficient pains had been taken. As it was, only two or three individuals gratified me in this respect, but in each case the eggs failed to develop. Female prawns were therefore taken, with eggs in very early stages of development, and kept under observation in an aquarium, for the length of time required. The ova were carefully removed from the pleopods, and hardened at intervals of from one to several hours, according to the age of the embryo. By obtaining a number of series in this manner, the whole life history could be traced in detail.

The breeding season of Alpheus begins at Beaufort, N.C., about April 1st. It covered the period of our stay at Nassau. (March to July) and probably began earlier and lasted later. There, the temperature is high and very constant (70° Fah. in March, 80° in June), and consequently the first phases are passed rapidly. It therefore rarely happened that a prawn was taken with eggs in an earlier stage than that of yolk segmentation.

Experience in using Perenyi's fluid for hardening the

[illegible] led me to discard this reagent altogether, and to substitute Kleinenberg's Picro-sulphuric acid, made upeither with water or weak alcohol(30%). The latter works equally well and economizes time. Perenyi's fluid seems too violent and uneven in its action, serving fairly well in some cases, but generally swelling out the chorion, and distorting the embryo by too rapid endosmosis. If the eggs are transferred directly from alcohol to alcoholic picro-sulphuric acid, they usually retain their normal shape, and can then be placed in alcohol of a higher grade, for permanent preservation. If however they are carried from the hardening fluid to weak alcohol, distortion is sure to ensue.

Preparations of the entire embryo as well as sections were made, but very little was attempted with the living egg. For surfacepreparations the hardened ova were first punctured to allow the fluids to penetrate the chorion more rapidly, and then stained entire, in Kleinenberg's haemotoxylon. They were afterwards shelled, where this was possible; saturated with paraffin by the turpentine-paraffin method, and carefully oriented in the block, with a hand lens. This last important process was rendered easy by the differential property of the stain, which affects only the embryonic cells, and leaves the yolk,

(in preserved eggs of a light straw-color), unaltered. The embryo was then cut away from the egg by the microtome razor, attached to the slide and mounted in balsam. All the drawings of surface views were made from objects, thus prepared.

In general, haemotoxylon is the best neuclear staining fluid, and it is especially useful in those cases, where the massive yolk contains numerous elements, the relations of which it is important to determine. The carmines are also serviceable but of less value. Soda carmine (Beccari's formula) proved to be incapable of removing pigment from the eyes, although it is especially recommended for this purpose. Perenyi's fluid is sometimes available for swelling out the chorion, and thus aiding in its removal, when this is desirable, although the embryo is liable to injury. It is also helpful in studying the egg with low powers. The food yolk which is often dark green, is affected less actively by this reagent than the embryonic tissue, while the latter is turned to a waxen whiteness and is thus well differentiated. More tardily the yolk is acted on, and becomes pink, and finally light yellow, after preservation in alcohol.

The original plan of making observations upon several other representatives of the crustacea for comparison with the more

detailed description of Alpheus, has, as yet, been only partially out. The early stages of Stenopus and Pontonia domestica, both obtained at Nassau, have however been followed, and also less completely, those of Hippa talpoides and Palaemonetes vulgaris.

PART FIRST.

DEVELOPMENT OF THE EMBRYO AS A WHOLE.

I

ORIGIN OF OVARIAN EGGS IN ALPHEUS.

The ovaries of Alpheus praecox are paired cylindrical bodies, lying close together between the alimentary tract and dorsal surface of the body. They extend from just behind the eyes to the end of the 3rd or 4th abdominal somite, and owing to the transparency of the skin of this species are extremely conspicuous, giving to the female an intense green or yellow hue, according to the color of the egg. The oviducts open in the usual way by a slit-like valve, situated on the basal joint of the 3rd pereiopod.

A transverse section of the adult ovary of this species is shown by Fig. 11. It passes through the thoracic region, close to the abdomen. These developing ova are between 2 and 3 days old, that is this interval has elapsed since the eggs now attached to the abdomen were laid, as shown by the state of growth of the latter. The ovaries are ripe by the time the young are ready to leave the egg, and the new ova are laid a few hours after the hatching of the zoëa brood.

The walls (Fig. 11, O.W.) of the ovarian tubes are thin sheets of connective tissue, which unite or meet on the middle line between the alimentary canal (Al. C.), and the dorsal bloodvessel (D.A.) The follicles lie loosely within these. The spaces (B.S.), (perhaps greater than in life), are filled with blood, or a coagulable perivisceral fluid, which also bathes the ovarian sacs. In this, blood corpuscles (B.C.) are usually found. The internal epithelium (F.E.) of the ovary, (the relations of which to the walls may be somewhat changed by the hardening fluid), is composed of large cells, the boundaries of which are probably distinct in life, with oval neuclei. The egg originates from these cells, whether from the whole cell or from the neucleus alone, is not so clear, as in the case of the lobster soon to be mentioned.

The ova begin their development in the lower median side (Ger.) of each ovarian sac, but after the eggs then filling the ovary are laid, this germ area or germogen passes upward to the position (Ger.) shown in the figure. This portion is surrounded by a thin capsule (E.E'.) of connective tissue, or follicular epithelium, consisting of fibres and flattened nuclei. The youngest egg (o) here shown, consists of a germinal vesicle, which corresponds to the nucleus of the follicle cell, and of a granular yolk-body

derived either from the cell protoplasm, or developed independently about the nucleus. Between [illegible] and [illegible]′, various stages occur. The nucleus (G.V.) which is filled with chromatin grains, at first grows more rapidly than the yolk body (Y.), but the latter soon gains the ascendancy. However in the ovum (of 1/300 inch in diam.) the germinal vesicle is relatively very large, its diameter being one-half that of the entire egg. The chromatin bodies gradually increase in size, until in an egg like the last, there are 6 or more large germinal dots, besides numerous granules. The food yolk at this stage is quite homogeneous, but may contain vacuoles (Vac.) The oldest eggs (a′ and [illegible]) are spherical and are surrounded by a delicate membrane, the future chorion (Ch.), or egg shell, which is a chitenous structure, secreted by the cells of the follicular envelope.

In the ripe ovary of this Alpheus the mature eggs, vitellogen (Vit.) fill the whole sac, excepting the lower median portion (Ge′.), where as already stated, the young eggs appear. Some 8 to 10 eggs are cut in a section of an average sized sac. They are closely crowded, and consequently very irregular in shape, and their bulk greatly distends the body of the prawn. The chorion, which is now fully formed, functions as a primary egg case,

and is the only membrane around the egg, nor is there any space between it and the vitellus. The food yolk is composed of spherules (usually fused together in preparation) and abundant vesicles, which likely enough, represent oily constituents soluble in alcohol and turpentine. The ripe egg is without a visible nucleus or germinal vesicle, but this is reconstructed after the egg is laid, even if fertilization does not occur.

HOMARUS AMERICANUS.

The lobster's ovaries are two solid rods of tissue, united anteriorly by a transverse bar. They have the appearance of an elongated letter H, and are usually dark olive green. Figure 6 is a drawing of the inner portion of a section through the posterior end of a lobe of the ovary, taken from a lobster in January, and Fig. 3, shows the central area (Ger. Fig. 6.) of a similar section under a higher power. The diameter of the entire section is one-fourth of an inch, or about twice that of the part represented in Fig. 3. The germogen (Ger.) which is the centre of dispersion of new ova, lies in the long axis of the lobe, surrounded by eggs in various stages of maturity.* We can therefore trace in a single good section at this stage, the evolution of the egg from the indifferent nucleus of the follicular epithelium, through

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* (The eggs of the oldest or peripheral tier are packed in radial order, so that the long axis of each is perpendicular to the ovarian wall.)

every phase, to the large, nearly ripe, [illegible].

In this form, the egg is descended from the indifferent nuclei (Fig. 3, I.E.) of the connective tissue stroma (St.S. Fig 3). The ovary is richly supplied with blood, being penetrated in all its parts, by blood sinuses (Bl.S. Fig. 3 & 6.), which are much more definite channels than the blood spaces noticed in Alpheus, and are bounded by chitenous walls (Ch.W.) of considerable thickness in certain parts. Within these channels elements of blood corpuscles (B.C.) and coagulated plasma are everywhere met with. The blood cells (Fig. 3, B.C. Compare also Figs. 11, & 19.) are distinguished from other cells of the body by its histological characters. It has a clear hyaline body of irregular form, and deeply stained nucleus. Some of these corpuscles may find their way to the ovarian tissue (Fig. 3B.C.) but this is not common.

The stroma (Fig. 3, St.S.) of the ovary is a syncytium of fibres and nuclei. The ordinary indifferent nucleus (Fig. 3 I.E.) is an oval granular body. Some of these (6.) surround the developing egg, and form the pocket or membrane of the egg follicle. Others are directly converted into ova. The various steps of this process are illustrated in Fig. 3. These nuclei (o′, o²) swell out, gradually becoming spherical, and are distinguished by the

characteristic appearance of their chromatin.

This is not so diffuse but is aggregated into coarse strings. The nucleus becomes the germinal vesicle of the ovum, and soon acquires definite characters. It develops an outer granular zone(3., 4. 5) which is the rudimentary yolk, and at about the same time an external fibrous layer appears, the first trace of the follicular coat. (F. C.) In an older egg (7.) all these structures are present, and the nucleus or "germinal vesicle", with its single germinal dot has the typical appearance. (Compare this egg with 5). It is not unlikely that these young eggs possess the power of independent motion. Amoeboid movements have been observed in the immature ova of several crustacea. At any rate as soon as development commences the eggs begin to pass outward in the sheets of stroma, between the blood sinuses. Vitelline spherules are soon formed in the granular yolk([illegible],) as the germinal vesicle attains its maximum size, and the egg continues to grow by accession to the vitellus. The vesicle has a distinct membrane (the wall of the nucleus) and lies at the centre of the egg. It contains stellate masses of chromatin and a single large refractive dot, which always takes a central position. A few large yolk spherules usually lie in

the young ones, in the ovary,(Fig.6),the nucleus is surrounded by a [illegible],of small and quite uniform yolk spherules,(this body of yolk material lying in a slightly paler zone), giving an appear-[illegible] of lighter [illegible]. The chorion (Fig.6 Ch.) is present, as in Alpheus. It is a delicate membrane lying between the yolk and the layer of follicle cells (Fig.6,f.c.),of which it is the product.

PALINURUS INTERRUPTUS.

The ovaries of the spiny or rock lobster resemble those of Homarus. The outer wall is quite thick,and from within trabec-ulae or sheets of tissue,which partially divide the lobe into compartments. There is also in the specimen studied,an area of growth and dispersal of eggs,in each division of the ovary, instead of a single lateral germarium as in Alpheus, or single axial one, as in the common lobster. The ova originate similarly as in Homarus. The oldest ova are enveloped in a distinct sheath,and the food yolk appears nearly homogeneous or finely granular in preparations. There is not simply one nucleolus,but several of these bodies as in Alpheus. The number of eggs laid by this animal is very great indeed (probably hundreds of thousands.)The eggs are attached [illegible]

The color of the egg is a bright orange.

[illegible] lineata begins to spawn in June.

COMPARISON.

Ishikawa (15.) has described very fully the [illegible] and [illegible]genesis of the prawn Atyephyra compressa. He considers that the ovum originates from the inner lining of the ovary, and is at the beginning a cell with a nucleus, and one, two, or rarely three nucleoli". The mature egg has two membranes, one of which is due to " the hardening of the peripheral protoplasm of the egg ", while the other (chorion) is secreted by the epithelial cells of the oviduct, and [illegible] at the time the eggs are laid. The nucleus of the ripe egg is invisible.

It seems that there may be a mistake here in regard to the origin of the egg membranes, unless this is an unusual case.

The egg shell or chorion is deposited [illegible] to be secreted gradually during the growth of the egg within the ovary.

For this reason, the chorion may have [illegible] stratifications, and split into layers.

The large glandular cells found in the oviduct of Atyephyra probably secrete the viscid fluid, by which the eggs are attached to the swimmerets.

[illegible] in the [illegible] of [illegible] (C., [illegible]): "Das [illegible] ist in der [illegible] und [illegible] Kern und [illegible]. [illegible] finden eine [illegible] einer Hülle [illegible] Chitin [illegible], [illegible] und mit [illegible] Hülle [illegible]".

This description applies very well for Alpheus, excepting the number of [illegible], which varies with different [illegible].

The [illegible] of Alpheus is covered by a [illegible], the origin of which seems to be undetermined. According to [illegible], however, it is not known whether this [illegible] is [illegible] by the follicular [illegible]. [illegible] (C.), [illegible] that it is formed between the [illegible] and [illegible].

The [illegible] pass [illegible] the [illegible] of the [illegible] is [illegible] of the [illegible]. This [illegible] undoubtedly the [illegible] for [illegible] of the [illegible] the [illegible]-

[illegible] obliteration.

Kingsley (25.) says of the common shrimp Crangon [illegible] that the recently laid ova differ only slightly from the later ovarian eggs. It is enveloped by a very thin structureless membrane, inside of which I have found no traces of an inner or vitelline membrane, as [illegible] may appear between the yolk and the [illegible]. Ludwig's general statement [illegible] of the [illegible] by [illegible] (Dotterhaut) the product of the [illegible], [illegible]. [illegible] primary [illegible], apparently very little work had been done on the [illegible] of egg membranes. Ludwig thus defines "primary" and "secondary" [illegible]: "Die primären Eihüllen [illegible] [illegible] bei den [illegible], [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible]."

[illegible] ; [illegible] T [illegible]

[illegible] during [illegible]

Each product of the first nucleus has developed a swarm of spores (S. S. Fig. 12, 13.) which arise by endogenous cell division in whole or in part. Four of these spore-swarms are cut in one of the sections (Fig. 12.), and a single one is seen highly magnified in Fig. 13. They form hollow spheres, which are suspended in clear areas of plasma. The yolk segments superficially about the spore-mass, just as it does about a single nucleus to form a pyramid in the centrolecithal egg. This is well shown in some sections. The segmentation is, however, not regular. In one case there were two large segments, nearly dividing the egg in two, besides several smaller ones. Each part contains one or more nuclear bodies, which consist either of spores, or of a peculiar reticulated mass of chromatin. Clear areas may also occur without spores.

About 8 spore-masses were present in the egg from which Fig. 12. was taken. Their character is best seen in Fig. 13. The protoplasmic area is pretty sharply defined. The spores vary in sizefrom refringent particles, to bodies of ordinary nuclear appearance. In the larger of these the chromatin is disposed in coarse grains. The yolk is vacuolated, and the spherules (Fig. 13. Y. S.) have the same appearance as in earlier stages.

How are these spore-masses formed? The answer to this question is given, I believe, by Figs. 25. & 26., which represent sections of one of the clear areas in the same egg from which the other drawings were made. The yolk (Y.) is not indicated. This clear field (Figs. 25. 26. P. A.) has several sporulating cells near its border. The larger (S. C.) is included in several sections. In one portion of it (Fig. 25.) there are two nucleolar bodies, besides numerous granules. A small spore with indefinite body, (Fig. 25.) (S. C.^{2}), lies on the border below it. In Fig. 26., the next section but one of the series, the cell S. C. which is cut again, is at this point of greater interest. This body is evidently discharging through its broken down wall, numberless minute elements (S.) into the clear field. On opposite sides, other smaller bodies occur, (S. C. 3-4) which differ only in point of size from the larger ones.

Further, in Fig. 22. a small protoplasmic area occurs in which a single spore-cell lies. This has one large chromatin mass, besides numerous microsomata. Figs. 5. & 23. are also from the same egg, the first showing the section with more detail. Here we see structures, similar to those already described. They are swollen bladder-like corpuscles, surrounded by yolk

(Y.S.),and consist of a fine reticulum,in which is suspended usually one large and great numbers of smaller chromatin particles. Various stages of growth are represented,so that it is probable that they arise from spores,and may in time become other cells of other spores. It thus appears that the hollow spore [illegible] (Fig.13,) may be formed by endogenous cell division from one or more other cells,which come in contact with plasma, generated in the yolk. These parent cells are derived from the first nucleus,probably by a similar process.

In the last phase obtained(Fig.29.),the whole egg is filled with several thousand very large elements,which are descended more or less directly,from the bodies just considered. They are now coarsely granular. The yolk is irregularly segmented, apparently with reference to these bodies,into blocks or balls (Y.B.). A blastoderm is not yet definitely formed.

This case is interesting when we compare with it ,the endogenous cell formation to be described in another section,and from a cytological point of view,it deserves more careful study.

DEVELOPMENT of ALPHEUS.

1st. to 6th. Phase.

1st Phase.

SEGMENTATION to FORMATION of the BLASTODERM.

(Figs. 1, 4, 9, 10, 15, 17, 24, 27, 28, 30, 31.)

The observations relate to the two species of Alpheus already mentioned, and as the development of each is the same, they will be treated as one form. The principal difference is in the size of the egg, or relative amount of food yolk.

In June, two females of Alpheus praecox laid eggs in an aquarium. These ova were unfertilized and most of them did not adhere to the pleopods.

A section through one of these infertile eggs, hardened about 5 hours after it was laid, is shown in Fig. 17. The nucleus or germinal vesicle has reappeared, although, as we have seen, it is not visible in ~~natural~~ mature ovarian eggs. Exactly when this happens I did not determine. It consists of clear plasm without definite bounds, and chromatin granules. The nutritive yolk is composed of (1) homogeneous corpuscles, of uniform size, excepting at the peripheral part of the egg, where they are much smaller; (2.) of small vacuoles, which presumably

represent elements, soluble in the reagents employed.

These lacunae occur in ovarian eggs, but are sometimes absent. There is a single egg membrane, (excepting that by which the ovum is attached to the ~~basis~~ hairs of the swimmeret, and which invests only a part of the surface), namely the egg shell or chorion. This is tough, elastic and very distensible, as shown by the passage of the eggs through the oviducts, and by the effects of reagents. It often splits into layers (Fig. 17. Ch.)), and is sufficiently transparent for surface observation of parts below it. These eggs, if unfertilized, are incapable of initiating the process of segmentation.

The first nucleus is shown in Fig. 16. It lies at the centre of the egg, and is elongated, previous to division. Relatively it is very small (Compare with it, Sinus, Fig. 14.), of definite outline, granular, and is imbedded in a plasma, which extends into the yolk. A coagulated fluid sometimes occurs between the egg-shell and the yolk, but normally the chorion closely invests the vitellus.

The nucleus now divides into 2, 4, and 8, parts. The last phase is illustrated by Figs. 9. 28. & 30. Intervening stages have been met with in other forms (Palaemonetes, Pontonia.)

where the process is similar.

Fig. 9. shows a section of the entire egg, in which 3. out of the 8. nuclei present are cut. The most important point to notice here is that the nuclei have travelled toward the surface, and are already visible from the exterior, but the yolk, (represented somewhat diagrammatically in Fig. 9.), is still unsegmented. One nucleus (X.), shown in detail in Fig. 30., is about to divide parallel with the surface, while another (Fig. 28.) is undergoing kinesis in an opposite plane. The yolk has suffered as yet, but little change. The largest corpuscles lie at the centre of the egg, and are more angular in form. No vacuoles appear in this specimen. A delicate granular layer is sometimes present between the yolk and chorion, and if normal, probably represents the yolk plasm, which is distributed through the egg.

The next, or 4th. segmentation stage, is shown in Fig. 10., where we now see the yolk divided at the surface into 16. blastomeres. It is therefore evident that this cleavage of the yolk takes place simultaneously after the 8. nuclei of Fig. 9., have undergone kinesis. This segmentation is regular, but only partial, since the great mass of yolk below the surface is not involved. We may regard the superficial blastomeres as cells

in a strict morphological sense. Each of these elements, or yolk pyramids, as they are sometimes called, has a polygonal base, near the middle of which, surrounded by food yolk, lies a nucleus, (Fig. 10.) The apices of the pyramid, if present, would meet at the centreof the egg, or segmentation cavity, which is filled with yolk. The nucleus is large and granular, and is suspended in a stellate or reticulate body.

The formation of the blastoderm or primitive skin, consists simply in the multiplication, and consequent reduction in size, of these huge deutoplasmic elements, until the surface has the appearance of a fine mosaic of hegagonal plates or cells, the nuclei of which lie quite at the surface, underneath the chorion.

Figs. 15. & 31. give one of the stages in this process, (Compare also Figs. 1. & 4.). About 32. cells or pyramids are now formed, and the dividing wall or septum (Sep.) between them, is extended farther into the yolk. The wall is continuous with a delicate layer (S.W. Fig. 31.). Part of a section of the series from which Fig. 15. was taken, forming the convex face of each pyramid. The nuclei have advanced farther toward the surface, and their long axes lie parallel with it. The inner ends of certain cells are cut in the middle of the section represented in Fig. 15. This egg happened to be in a period of rest,

while in others the nuclei are actively dividing, and now always radially, or at right angles to the surface. The cells continue to multiply by geometrical ratio, until upwards of 256. are formed, and a blastodermic envelope is established in the way described. It is important to note that all products of the first nucleus reach the surface, and take part in forming the blastoderm.

2nd. Phase.

MIGRATION of CELLS from the BLASTODERM.

THE GASTRULA. Figs. 37-55., 57.

In an egg 13. hours older than the last, there are cells scattered through the yolk. The pyramids are about one third as large as those in Fig. 15., and the nucleus of each is not yet quite even with the surface. Up to about this time, segmentation has been regular, and at the close of the first phase of development, the egg was radially symmetrical. Now however, the rate of cell division is accelerated over one portion of the egg, and perhaps correspondingly retarded over the remaining surface, so that a germinal streak or disc, corresponding to the future embryo, is differentiated from the blastoderm, and the egg becomes two sided. As already indicated, a migration of

cells from the surface to the interior of the yolk takes place. The egg, as it appears, when seen from the side of the germinal disc (G.D.), is shown in Fig.47. In obverse view it presents much fewer cells. (All the nuclei in this figure were drawn with the camera, excepting a few at the periphery.). Gastrulation soon follows this stage at a certain point in the area G.D.

The surface of this egg is best shown by a tangential section (Fig.48.), in which we see the hexagonal blastodermic cells, (Bd.C.) containing yolk (Y.), and an excentric nucleus.

The passage of nuclei into the yolk is illustrated by a series of 7. consecutive sections taken from a single egg. (Fig. 38-44.) Figure 38 cuts 6 nuclei, one of which has wandered a considerable distance into the interior. In the next (Fig. 39.), two nuclei are caught in the process of tangential division (a, a^2.); one (a^2.) has just entered the yolk, and a fourth is in the centre of the egg. Nuclei, a, a^{2-3} are hit again in the succeeding Fig. 40. Various phases of this process are shown by the other members of this series. The yolk is represented in Fig. 45. (The 4th in series after Fig. 44.), and the septa between the surface pyramids are still apparent (Sep.).

An enlarged portion of another section is given in Fig. 37, where several nuclei are seen to be flush with the surface, while others have moved below it. The yolk (Y.S.) is fragmented around these elements, and their external protoplasm is without definite bounds. These wandering cells pass to the centre of the egg, and the yolk becomes aggregated around them, in the form of blocks or irregular balls. This condition is indicated in Fig. 46., taken from another species. Fig. 57. is from a slightly older egg (20½ hours older than the yolk pyramid stage in Fig. 15.). The section passes through the embryonic disc (G.D.), the cells of which are now more numerous, and closer together. The septa (Sep.) between the pyramidal cells may yet be distinguished. The egg gastrula stage immediately follows. A slight depression occurs at the hinder end of the germinal area, due to the sinking down of the blastoderm at that point. This invagination, slight as it is, represents the primitive digestive cavity or archenteron, and its mouth, the blastopore. The egg is now a modified gastrula. In some forms, as the cray-fish, the gastrula cavity becomes a closed chamber in the yolk, and is converted into the mesenteron or midgut. In Alpheus however, and in Decapods generally, the archenteron

soon disappears, and the mid gut is formed independently, at a later period. A line drawn through the blastopore and middle of the germinal disc, makes the long axis of the future embryo.

The simple structure of the gastrula embryo is illustrated by a series of transverse sections. (Figs. 49-55.).
The cells in the centre of the egg (Y.C.) represent the elements which migrated from the blastoderm prior to gastrulation.
These are quite large, granular bodies, and in some cases, lie within the yolk balls. In Fig. 49, the posterior edge of the gastrula embryo is cut, and the succeeding sections pass through the primitive mouth or blastopore. Fig. 52, is the entire section, of which Fig. 51, is a part. The small pyramidal cells, forming the floor of the gastrula depression, now contains no deutoplasm, at their peripheral ends. Their nuclei are placed at the deeper parts of the cells next to the finely divided yolk, where the cell boundaries are lost. Moreover numerous elements (b, b^{1-5},), Figs. 52-54., have wandered from the floor of the cavity into the egg, or forward under the germinal disc (G.D, Fig. 54.) These cells have a peculiar histological character. The nucleus is spherical, and contains coarse grains of chromatin. They are all united by protoplasmic processes, which form

a coarse reticulum. The germinal disc is one cell thick excepting near the gastrula mouth, as shown by Fig. 55., which passes through its anterior half.

The first step toward the formation of the germinal layers has now been taken.

We may distinguish (1) a superficial epidermis, or ectoderm (Ep.) composed of flattened lenticular cells, representing the parts of the blastoderm which took no part in invagination, and (2.) an inner undifferentiated layer, corresponding to both endoderm and mesoderm, including all the remaining cells of the egg. These latter it will be remembered, are derived from two sources, namely (a.) from the blastoderm before gastrulation, and (b.) from the invaginate cells of the gastrula.

3rd. Phase.

OPTIC DISCS and ABDOMINAL PLATE.

Figs. 56-69.

This stage is characterized by the growth of the abdominal plate, due to a thickening of ectoderm in front of the blastopore, and simultaneous forward growth of invaginate cells below the surface; and ~~to~~ by the appearance of the optic discs; two patches of ectoderm, one on either side the median line. The last mark the forward, anterior extension of the embryo.

When a living egg is examined by reflect~~ive~~ed light, these structures appear as misty white patches, (Compare Fig. 2.) lying near together. Fig. 58. is from a surface preparation of such an embryo. The principal cell mass (Ab. P.) is the abdominal plate, from which the abdomen and possibly a part of the thorax is afterwards developed. The blastopore has now closed, but its position (Bp.) can be easily determined.

The optic discs are due to the rapid spreading of ectoderm cells from definite centres. They are joined to the abdominal plate by a lateral cord (L. Cd.), on which the appendages are subsequently budded off. A transverse cord (T. Cd.), soon unites the two optic discs anteriorly, and thus encloses a

central triangular space, of undifferentiated cells which correspond to the sternal region of the animal.

The forward extension of the invaginated cells, is indicated by the shaded elements (P.M.) They advance forward as well as upward into the yolk in two lines, from the abdominal plate toward the optic discs. In this species of Alpheus, the embryo cover nearly one hemisphere of the egg, and the angle between the optic discs, varies greatly in ova from the same prawn.

The embryo at this phase occupies a considerably larger space, than it does a little later. In other words it undergoes a marked contraction, becoming smaller. This is not so evident in the figures, but it is very noticeable when a series of different stages are compared. This remarkable phenomenon has been noticed in several decapods, and Kingsley has advanced a theory to account for it. If we notice also in Figs. 109. 110, the older embryo is the smaller of the two. This last may be an exceptional case. The embryos from the same prawn often very considerably in size. As I have made no detailed measurements, I therefore will merely mention the fact.

When we study the structure of this embryo, (Fig. 58. 59. 60.), we find that with the greater extension of the primitive

primitive epidermis, there has been a corresponding, or even greater activity among the internal cells or inner layer as we may call them, remembering that from these later the meso-derm and endoderm are ultimately formed. The longitudinal sections just referred to, including the whole egg, show best their relations. We can still distinguish, as in figure 60, primary yolk cells (P.Y.C.) from the secondary element (S.Y.C.) derived from the invaginate gastrula. The first are large granular bodies which have wandered to distant parts in the egg. Later however, it is not possible to distinguish them, and the two kinds are indeed from the first morphologically, if not physiologically, quite similar. The internal yolk is irregularly segmented into blocks, more noticeably than in the previous stage. At this point it is plain that the elements of the egg present several stadia of organization (Fig. 15.), the structural unit was a large yolk pyramid or cell, with a peripheral nucleus. The blastoderm cells, and in fact all the ectodermal elements, with definite nuclei and cell-boundaries, are the direct descendants of these blastomeres, and are cells in the ordinary sense. The invaginate cells moreover, form a syncytium below the ectoderm of the abdominal plate (A.P. Fig. 50), as already shown.

Further some of the nuclei enter the yolk and play the role of independent cells. The yolk ball is not strictly homologous with a yolk pyramid, inasmuch as the nuclei of the former, multiply without reference to the surrounding yolk mass.

We may therefore regard all independent yolk elements, and all the elements of the egg in fact, as equal physiological units, whether there is a definite protoplasmic cell body or not, and speak of them as cells without causing confusion, inasmuch as it is rarely necessary to make a morphological distinction, (See Section 5.) The lateral section in Fig. 56., passes through the outer edge of the abdominal plate, and the next toward the middle line crosses the lateral wing of yolk cells (C.Y C Fig. 60.) Fig. 59 is from a median longitudinal section through the embryo and the egg, cut in the abdominal plate through the point where the blastopore (B.) was situated. We see by a glance at the figures, that the yolk cells pervade the greater part of the vitellus. They pass in all directions from the abdominal plate, but chiefly upward to each side of the latter. Some of these elements on the other hand ([illegible].Y.C′ Fig 59), are creeping forward under the embryonic rudiment.

The flattened cells of the primitive yolk-layer (Ep.) are plainly differentiated from the inner layer. These lenticular bodies are frequently carried away with section (Fig. 56, 60, Ep′) where this is separated from the yolk in preparations.

The structures present at this stage are further illustrated by a highly magnified portion of a median section through the abdominal plate (Fig. 63), and by a series of transverse sections (Figs. 61, 62, 68, 69). In Fig. 61 the abdominal plate is sectioned somewhat obliquely to the vertical plane, in a posterior direction, and but few yolk cells are met. The section in front of this (Fig. 62) crosses the lateral cord (L.Cd.), and numerous large yolk elements are found in the interior of the egg. Anteriorly the optic discs (Figs. 68, 69, O.D.) are traversed, and below them several yolk cells. Septa (Sp.) extending from entodermal cells into the yolk, still indicate the columnar or pyramidal structure of this primitive layer.

The character of the cells of the abdominal plate is given in more detail by Fig. 63. Here we see numerous very characteristic bodies (Y.C.) lying below the ectoderm, which are histologically distinct from the ordinary cells of the layer. After the closure and disappearance of the blastopore, the cel-

the lamina near that point come up to just below the surface, and help build up the abdominal rudiment which is continually adding daughter cells into the yolk.

This point will be made clear in the next stage. The boundaries of these wandering cells are lost, or nearly so, they become larger and spherical, and the chromatin in each (at a certain stage) is disposed in coarse grains.

The vitellus is finely divided in the presence of the actively multiplying cells, and the larger so pushed apart are separated into balls (Y.B.) round numerous yolk elements.

Up to this time no ectodermal thickening has occured in any part of the embryo, excepting the abdominal plate.

The optic disc consists of a single layer of flat polygonal cells. This is well shown by the series of consecutive transverse sections, (Fig. 64-67.) passing through the disc O.D. in an antero-posterior direction.

The cell walls are distinct, and the long axis of each nucleus lies parallel with the surface. When the cell divides, this position is reversed, the major axis of the cell being then perpendicular to the surface, and the plane of division always tangential.

From the optic disc the eye and its ganglia are poorly developed. An important change in these rudimentary organs appears in the next stage.

4th Phase.

THICKENING of OPTIC DISC, RUDIMENTS of APPENDAGES.

Figs. 70-85.

A surface view of an embryo and egg, a few hours older than the last, is shown in Fig. 72. The lateral cord (L.C.), forms a complete bridge between the optic area and abdominal plate, and on it two centres of active cell growth have arisen. One of these, near the optic disc, is the beginning of the first pair of antennae (A.I.), the other, the first trace of the mandibles (Md.), close to the rudimentary abdomen. Some of the central cells, concerned in the thickening of the optic disc, are characterized by their large size. The transverse cord (T.C.) is now partially developed. The embryo is V shaped, and the unclosed sternal portion is still imperfectly covered.

Glancing now at a series of longitudinal sections through the egg at this stage (Figs. 70, 71-[illegible]5.), we find that while the area of the abdominal plate (A.P.) is increased, the cell mass below it is not proportionately enlarged.

It has however, sent forth into the vitellus, a swarm of elements, all of which are large and granular, and it is no longer possible to distinguish with certainty between primary and secondary yolk cells. These bodies multiply in the egg, and spread to all its parts. Nuclear figures of dividing yolk cells are sometimes seen in Fig. 75. (Y $\overset{2}{C}$) Here we find some of these (Y.$\overset{\prime}{C}$.) passing forward, underneath the embryo, and others (Y.) moving in an opposite direction, toward the surface of the egg. Fig. 75 represents a nearly median, longitudinal section through the transverse cord, and abdominal plate. In Fig. 71. two yolk elements (Y.$\overset{\prime}{C}$.) are found, approaching the lateral cords, and in the section (Fig. 70.) which cuts the optic disc through the middle, another cell is met with, close to the latter.

The structure of the abdominal plate is given in more detail in Fig. 85, at a point anterior to the primitive gastrula mouth. This illustrates the character of the syncitium already referred to, and shows very well the fine degree of fragmentation which the yolk corpuscles suffer in the presence of the protoplasm. The walls of contiguous cells are distinct, at the surface, but below it, this is not the case. Here the cell protoplasm forms a net, which engulfs in its meshes innumerable yolk

particles, which are probably directly absorbed. Under these favorable conditions of nourishment, the nuclei grow rapidly, and spread to various parts of the egg. Very few karyokinetic figures were seen among these bodies, a fact which further indicates that many of them pass into the yolk. The irregular tier of cells at the surface of this section indicates, as stated before, that after the closure of the blastopore, cells continue to migrate from the surface at that point.

Certain of these cells (c. c.) are dividing in the usual way, that is in a plane parallel with the surface, (by which the superficial area of the part is extended), while others (c. c^2.) appear to be splitting in the opposite plane, or to be crowded below the surface (c. c^3), thus increasing the thickness of the plate.

The nuclei of the latter contain, besides coarse granules, several large nuclear bodies.

The process by which the thickening of the optic disc is effected at this stage, is well shown in a series of consecutive sections, passing through this area. (Figs. 76-83.). The anterior edge of the disc is cut in Fig. 76, while the last of the series, Fig. 83, intersects the rudiment of the first antenna.

This thickening is primarily due to the crowding below the surface of ectoderm cells, caused probably by their rapid division in planes ~~parallel with~~ perpendicular to the surface. This is an important point, since it involves the question of the eye and its ganglia, and will be referred to again. The boundaries between superficial cells are well marked, and a nucleus which has passed below the surface is for a time invested by a distinct somatic layer (Fig. 80, c.) The relation of the optic disc to the whole egg is shown in Fig. 84., (the left part of which is seen enlarged in Fig. 80.) The yolk at this level is segmented, and contains cells, none of which however, have approached near to the disc.

5th. Phase.

RUDIMENTS of THREE PAIRS of APPENDAGES.

OPTIC DISCS united by a TRANSVERSE CORD.

[illegible], and [illegible] CELL-FORMATION. FIGS. 86--10[illegible].

We reach at this point a critical period of development, and the reader who has followed me thus far, will find that the peculiar behaviour of the wandering yolk cells, and other conditions now present, become more intelligible during this phase. As regards germinal layers we have shown that there is now (1) an outer ectoderm, (2) an inner indifferent layer which for the most part represents mesoderm and endoderm. The first of these is well defined both by its position and histological character. It is one cell thick over the greater portion of the embryo and egg, and the boundaries between the elements are well defined, as they are between the yolk pyramids, at an earlier date. A thickening of this layer is already begun in the centre of the optic disc, and the abdominal plate continues to receive new recruits from the surface.

The second germinal layer, which is not a layer of course, in the strict sense of the term, includes all cells scattered

through the yolk mass, together with those found at any time below the surface, of the abdominal plate, from which part many of the yolk cells have emigrated. The origin of this layer is accordingly threefold, since its elements are derived (1) from the blastoderm before invagination: (2) from the cells lining the shallow pit of the gastrula cavity, and their products: (3) from ectoderm cells which are subsequently crowded in from the surface near the position of the former blastopore; probably just anterior to this point (v. Fig. 58.).

This second cell-aggregate, called the inner layer merely in a topographical sense, is, up to this time, undifferentiated, and cannot be divided, if my interpretation is correct, even artificially into one or more sets of elements. I find it impossible to make even a histological distinction between them beyond a certain stage (v. Fig. 73. & 74.). They are in fact potentially both epithelium, muscle and gland, since they give rise to all these tissues. The bulk of them form the mesoderm, while some (the endoderm) remain in the yolk and subsequently give rise, in whole or part, to the lining of the mesenteron, and what is rather surprising, other yolk cells again, pass to the extra-embryonic surface of the egg, and join the flat epithelial cells of that part.

These facts will be illustrated later on.

Taking up the line of development where we left it, in the 4th stage, we find that some important forward steps are now rapidly taken. The embryo, represented by Fig. 93. is approximately 3 days old (Temp. 78°.-80°.Fah.) It covers nearly one entire hemisphere of the egg, the opposite of which is sprinkled with flat epithelial cells, like those seen at the periphery in the figure. The nuclei were drawn with the camera, excepting those in the centre and at the edge of the field, from a surface preparation. The second pair of antennae have now appeared, and we therefore have the buds of the first three pairs of appendages (not counting the eyes) springing from the lateral cords. Each appears simply as a centre of cell proliferation.

In point of time all are developed nearly simultaneously, but the second pair of antennae seem to lag a little behind the rest. In this respect crustaceans vary much, as might be expected. The abdominal plate is a very conspicuous mass of cells behind the mandibles, which abut against it on either side. Some of the elements, seen from under the surface, are very large, a character which they earlier possessed. They spread out on either side, in the direction of the lateral strings.

The transverse cord (T.C.) representing the anterior part of the brain now completely bridges the gap between the optic discs. The ventral enclosed pit or sternal area, St.A., is by this time quite closed over. This is effected by a downward (that is posterior) excursion of cells of the transverse cord, and probably also by the approximation of the lateral cords, ~~of the transverse cord~~.

In the optic discs (O.D.) numerous large cells (C.M.) are seen, both at the surface and below it.

We recognize here an area of migration, or "multipolar" invagination analogous to that in the abdominal plate, and a thickening of ectoderm results in both cases.

Cell outlines, though apt to be indistinct in the preparations, can be usually made out, but it is not desirable to represent them in the figures.

The nuclei of the epithelial cells, or of the cells of the abdominal area, are spherical or oval, while those of other parts are mostly angular in contour. This is due to crowding, which has possibly altered the original arrangement of nuclei. At any rate, the systems of beautiful concentric rings, and trajectional curves are not so marked by any means, as they appear in Reichenbach's and Winter's masterly drawings of the cray-fish embryo.

Their representations are however, evidently disagreeing, and the embryonic organs of Astacus,are from the first, more diffuse,that is more widely separated than in Alpheus.

According to Reichenbach,the superficial ectoderm cells of the embryo crayfish multiply about a given centre,(as those of the optic disc "head-fold",or "thoracic abdominal plate"),in obedience to the trajectional law announced by Sachs and others, according to which nuclei always divide in two opposite directions,that is either radially from the centre,giving rise to a string of cells,or at right angles to this plane,thus producing new strings and building up a series of concentric circles or distinct lines of cells. The position of the equatorial plate of dividing nuclei,which some eggs of Alpheus show abundantly , indicate that this law is generally followed ,in the optic disc at any rate. Observations on this subject however, to be of any value ,should be made on very carefully preserved specimen ,where distortion from all sources has been reduced to a minimum. These conditions were unfortunately,not fully attained. Several transitional stages between this and the egg shown in Fig. 72., will not be considered. Fig. 86 & 87 88-90; & Fig. 91 ,are drawn from eggs taken from the same parent

and hardened at intervals of from 6, to 12 hours.

The series of longitudinal sections (Fig. 85-90.) have some interesting facts, especially with reference to the peculiar role of the yolk cells. The section in Fig. 88, is about median, the first continuous layer of ectoderm extends from the transverse canal (Tr. C.), to the characteristic cells of the rudimentary abdomen (Ab. P.) Some yolk elements (y. c.) passing from the latter, are nearly in contact with parts of the embryo.

The next section touches the outer edge of the abdominal plate, the large granular cells of which are distinct, and [illegible] the lateral cords and buds of the appendages. The folds of the latter, arise by the tucking or pushing in of superficial cells.

Here one yolk cell (y. c.^{1}) is ready to settle in the pocket of an appendage; another (y. c.^{2}) at a distant part of the egg, is in process of division, while still others (y. c.^{3}), have wandered in a diametrically opposite direction.

Again in Fig. 90, we see more of the elements. They are large, round, or irregular bodies, filled with coarse deeply staining masses of chromatin, with scarcely a trace of protoplasm between them and the yolk. In this case the majority of them are underneath or eccentrically above the embryo.

In the middle of the optic disc (Fig. 90, O.D.) the large granular cells (G.C.) visible from the surface in Fig. 93, are seen. One of these (gc.) has just been crowded below the surface. In an egg 6 hours older, a section through the optic area (Fig. 86, gives evidence of the greater increase of the latter emigration of cells from the surface, and it is not unlikely that some yolk elements (y.c.) have by this time joined it. In Fig. 87, the inner edge of an optic disc, and the outer border of the abdominal region are involved, showing that the ectoderm here is partly a single layer. The cell boundaries are clearly visible. Two large yolk cells are in contact with the embryo at this point, in line with the appendages.

Fig. 91, is drawn from an egg hardened 12 hours later. The plane of section passes obliquely through the optic discs, cutting the anterior half of one (to the left) and the posterior portion of the other. It shows us very plainly the fate of these peculiar yolk cells. Some lie just over the optic thickening, to which they join themselves, while others are near the outer surface of the egg, which one (y.c.) has quite reached, and will soon become indistinguishable from the ordinary epithelium Ep.)

The [illegible] elements, after [illegible] journey through the body in the embryo, are converted into muscles, and have formed definite layers. This will be seen presently.

The transverse cord (T.C.) is no longer a simple structure, and the large ganglion cells (T.M.) in the centre of the optic disc are most marked. Turning now to the eye already described (Fig. 93.), which forms the next link in the series, we find some important changes to record. (Fig. 92, 94-97.)

The optic areas (O.D.) have become cell masses of considerable size. Some of the large central cells just mentioned, appear in the longitudinal section (Fig. 96.) while the sections in the opposite plane, show clearly enough how the rudiment of the ~~[illegible]~~ eye and its ganglion, continue to be built up. One of the outer cells in Fig. 96., is dividing in the usual way (that is in a plane at right angles to the surface), while the position of the equatorial planes of two cells in Fig. 95., shows them to be splitting in the opposite direction. The crowding in of superficial cells resulting from the first method of division is plainly indicated in Fig. 94.

The thickening of the optic disc is therefore [illegible],

(1) mainly by emigration of cells from the [illegible]:

(2) partially by delamination, and (3) by the immigration of yolk cells. Further, it is possible that some of these elements may multiply by endogenous cell division, producing spores, which grow into cells. Spores ( ) make their appearance quite suddenly at this phase of development, and they explain at once the peculiarly coarse, granular structure of many of the embryonic cells in previous stages. (Compare Figs. 63 85 and others.). They appear in all the figures of this stage, and in nearly all parts of the embryo. Their history has been pretty fully traced. They originate by endogenous growth, chiefly in cells of the abdominal plate, and of the yolk. They probably correspond to the bodies termed "secondary nucleolar cells" by Reichenbach. Their origin and function will be discussed in a separate section. (4.).

The peculiar nature of the nuclei of the syncytium of the abdominal plate is still quite marked (V. Fig. 92). They are the largest elements in the egg, and each contains from one to several deeply staining bodies of chromatin. This cell mass has not increased at a rate corresponding with the general growth, owing presumably, to the fact that elements continue to be detached from it and to pass into the yolk. This also is probably still

[illegible] multiplication of these cells, and by the pushing in of those of the surface.

The fold of the [illegible] (Al, 'l, Fig. 96) [illegible] embryo 6 [illegible]. Figs. 98-100, represent a series of three longitudinal sections through [illegible] of this age. It [illegible] of the nauplius. The antennae resemble, in size and shape, the first pairs of rudimentary limbs. The abdominal fold is not yet formed, and the labrum is undeveloped.

The stomodeum (Fig. 98 St.) first makes its appearance as a slight depression of ectoderm in the middle line, between the [illegible] of the neural plate, in front of the 2nd antennae, as far as I can determine, considerably behind the first pair.

The number of spores (S) and sporulating cells (S.C.) has now very greatly increased. We find them in all parts of the embryo. The coarse granulation apparent in some of the [illegible] cells renders it probable that these bodies are potentially able to reproduce by spores. The section through the abdominal plate (A.P.) in Fig. 98, shows some points of interest. Many of its cells contain large spore-like bodies, similar to those [illegible] free in the yolk below.

Close beside a superficial cell, which is undergoing cleavage, there is another very large element ([illegible]), containing several spore like nucleolar bodies. This has evidently just been crowded down by its neighbors, from its original position at the surface.

The mesoderm is now a clearly defined layer, (Figs. 99& 100, Mes.) and its cells are slightly differentiated from the yolk elements, to which they owe their origin.

It stretches forward from the abdominal plate, in the form of two thin sheets or bands, along the line of the appendages. Its elements are flattened, and spindle shaped, the long axis of each is parallel with the surface, whereas the major axes of the ectodermal nuclei at this point are perpendicular to it.

The mesoderm is unsegmented, but its cells enter the pockets of the appendages, and they may multiply by spores.

6th. Phase.

THE EGG NAUPLIUS. Figs. 101--127.

The embryo has by this time acquired certain characters which strongly recall the free swimming nauplius of copepodal larvae. The fully grown egg nauplius is shown in Fig. 111. The steps which lead up to this from the point last reached must first be considered. The condition of an egg 12½ hours older than that last described, is illustrated by a series of five longitudinal sections (Figs. 101--105.) The fold of the abdomen is now recognizable (Fig. 104. Ab.), and the stomodaeum has grown down in the form of a straight, narrow tube, between the bases of the first and second pair of antennae (Fig. 105. Std.) The space between the level of the oesophagus and abdomen is occupied by yolk fragments, among which are interspersed numerous spheres (?) and wandering cells, derived from the abdominal fold region. The ectoderm over this part, corresponding to the sternal area (St. Ar.) shows a tendency to thicken. The nuclei of the outer layer are elongated, wedge-shaped bodies, which stand perpendicular to the surface, and are closely dove-tailed together with the ends of the wedges pointing either inward or outward. This indicates rapid cell division in one plane (viz. in that parallel with the surface.)

and result is the squeezing in cells here and there, and thus in thickening the layer. The bounds of the outer cells are quite sharp, and their nuclei like most of those of the egg, contain coarse granules.

The oesophagus develops into a relatively long, straight tube, with appreciable lumen, and it is soon surrounded with sparse and scattered mesoderm cells. It is formed before the primitive mouth and from 1 to 2 days before the proctod~~e~~rm.

The abdominal fold appears to arise by a cleft in the ectoderm. This is already noticeable in Fig. 104., but fully formed in Fig. 106. Its large cuneiform nuclei indicate the pressure to which its cells are subjected. The cleft is at first perpendicular to the surface, and co-extensive with the oesophagus, with which it is also parallel. This cleft does not at first extend quite across the abdominal area, but forms a deep transverse fissure, or pocket, as seen in Fig. 106, and ~~i~~ also in horizontal sections. It apparently does not begin by a true ingrowth of ectoderm from the surface, although there is eventually, a marked infolding of this layer. According to Kingsley (25) the abdominal fold begins in Crangon by an inpushing of ectoderm. The result in either case is the same. The relations of the parts of the embryo at

this phase, on the other hand, must be quite different in the two forms, judging from Fig. 11, of his paper.

Numerous elements below the abdominal fold, which we will now call mesoderm, continue to pass forward, underneath the embryo and to join the definite bands of this layer.

This sheet of mesoderm is well shown for one side, by Fig. 102, 103, Mes., Laterally, where masses of these cells enter the lobes of the appendages, the mesodermic band has a segmented appearance. Mesoderm cells which join the optic discs probably form connective tissue coverings to these parts although it is difficult to determine if all such cells are thus differentiated.

The four segments of the egg nauplius are clearly shown in Fig. 103, which passes through the optic areas, the lobes of the three appendages, and the edge of the abdomen. The similarity between them is equally marked, whether the embryo is viewed as a whole or studied by means of sections. So far as their development is concerned, there are good grounds for treating them as homologous parts. The appendage is primitively an outgrowth of ectoderm, with a thickened pad of ectoderm at its base, which becomes the nerve ganglion of the segment. The optic discs, which give rise to the eyes and its ganglia, are also due to a thickening of the epidermis.

One of the most recent writers on Arthropod embryology, Reichenbach, finds that in the crayfish the optic ganglia are developed like all the other ganglia of the brain and ventral nervous system, and he therefore gives them a segmental value. This subject will be considered in another place.

The structure of the optic disc is substantially the same as before. They consist of large cell masses, united by the thickened transverse cord (Fig. 107, T. Cd.) and covered below by a more or less definite layer of flat mesoderm cells (St. S.). The elements of the centre of the disc are still recognizable by their characteristic, large size. Growing spores appear in or near the rudiment. In Fig. 102, three ectodermal elements are caught in karyokinesis. Two of them lie close together in the optic tract, and are splitting in a radial direction; while the other, at the edge of the abdominal fold, is dividing in the usual way. In this connection it may be said that karyokinetic figures of dividing nuclei are very common in all stages from the first nucleus up to the most advanced condition. Naturally it is usual to find either great numbers of cells or none at all in this condition, according as the egg is in a passive or active state. In Alpheus minus, on the contrary, in case of the product

of the first nucleus at least, the division is evidently direct. Different species and genera of Arthropods must, however, be expected to differ in this respect, as in so many other points of detail. Reichenbach finds nuclear figures in abundance in Astacus, while Kingsley, in a recent paper on Crangon, states that he has seen nothing like karyokinesis, either in the segmentation or subsequent development of that prawn. Of course in any case, we study only the rapidly achieved result, and, except in the living egg, or in a pretty full series of embryos, a matter of this kind could be easily missed.

A median longitudinal section through an egg from the same prawn, but preserved a few hours later, (Fig. 106.) shows the cleft (Ab.C.) has been extended into a pouch, which thus marks off the abdominal fold (Ab.).

The ectoderm on the middle line both at the bottom of the cleft, and between it and the oesophagus, is generally not more than one cell thick. The area (St.A.), square-cornered in section, along which the ventral nervous system is to be developed, soon changes its form and position. (Compare Fig. 125.)

It now abuts in the eggshell, but is soon pushed beneath it, by the forward growth of the abdomen.

the latter, in time, comes to lie between this serosal or vitelline and the chorion. The Labrum (Lb.), which is here undeveloped, then grows forward, or rather backward to [illegible] the [illegible], carrying with it the position of the mouth, and lengthening the oesophageal tube until we have the relation seen in Fig. 125., which is from the egg next to be described.

The proctodeum is not yet very well defined, its [illegible] beginning at the point Pd., Fig. 106. (Fig. 126), is a transverse section at about this plane, from an egg intermediate between the two considered, and if I am not mistaken, we have here the first trace of this structure. An invagination is taking place here [illegible], (Fig. 126, Pd.), where the nuclei are seen to lie at the deeper ends of the cells. Their small size indicates rapid multiplication at this point. The invagination of the hind gut is at first solid or nearly so, it may be quite impossible at first to distinguish any lumen.

The relation of the embryo to the whole egg can be seen by reference to Fig. 108., which is taken from the same series as Fig. 106. The lateral thickening of ectoderm, [illegible] the rud-[illegible] [illegible] the [illegible] of the different [illegible] [illegible].

A layer of large cells (B.Z.) in the abdomen is quite noticeable at this time. This I suppose corresponds to the region Reichenbach described as "budding zone", and attributed considerable importance to, in Astacus, at a similar phase. According to this writer the abdominal fold or the tail (abdominal process) gives rise in the crayfish, not only to the abdomen proper, but to a part of the thorax as well, and new segments are added to those present in the egg-nauplius, by a process of "budding" from this zone. My observations on this subject are not, at present, sufficient to admit of an opinion as to the value of these cells in Alpheus.

Besides the chorion (Fig. 108.) which, in the living state, invests the egg closely, there is now evident a second delicate membrane (Th.) surrounding the entire egg (V. Fig. 104.) This is a secreted product of the blastoderm, and of pretty general occurrence among Arthropods. It has been regarded as a cuticular character, and morphologically equivalent to a first moult; what its real significance may be, I do not know. It does not conform to the fold of the abdomen, or to the oesophagus. It is a well marked egg-nauplius feature, but is not clearly defined much before this phase.

The yolk cells have decreased considerably in number. Two are seen in Fig. 108, quite near the surface of the egg. As already stated, some of these bodies ultimately reach the surface and become undistinguishable from the ordinary epithelium at this point. This is very well shown by a study of the series from which Fig. 105, was taken, where all stages in the process can be seen. A portion of one of these sections is given in Fig. 34, where two yolk cells (y. c.) already tangent to the surface, are undergoing flattening (V. Fig. 81 Y. C′)

The fully developed egg nauplius of Alpheus praecox (Fig11) is about a week old. It rests in one pole of the massive, oval or oblong egg, occupying a relatively very small part of the surface. Embryos from the same prawn vary considerably in size and shape, and somewhat also in degree of development. Thus in one of this set (Fig. 109.) the 2nd pair of antennae are bilobed and other parts are more developed. The specimen from which the drawing is made is about 1/80 inch long, and the entire egg if represented in same view, would be nearly twice the diameter of that portion of it given by the figure. The relation of this embryo to the egg is shown by Fig. 127, where the plane of section is through the long axis of the egg, but transverse with

respect to the embryo. (Compare also Fig. 109.)

The egg increases somewhat in size in the course of development, and also changes its shape in some species, being at first round, then, oval and oblong. The embryo caps one pole of the oval egg, so that the long axis of the former is parallel with the short axis of the latter. In course of growth however the head approximately retains its position at one end, while the body grows down one side of the egg, and reaches the other pole, so that the major axis of the embryo is now parallel with the long axis of the ovum. Most prominent now are the optic lobes (Fig. 111 O.L.), two large, oval masses of cells, which represent the optic discs, or the future eye-stalks. The eyes of most prawns attain to the stalked condition pretty soon after hatching, and in Astacus this condition is reached comparatively early in embryonic life, but in Alpheus the adult eye is never mobile, since it is covered by the carapace, and the stalk of the larval eye is never prominent. The block of cells (O.G.) in close relation to the first antennae and optic lobes, is the ganglion of the [illegible], and constitutes a great part of the future brain. It subsequently divides into two portions, an anterior, which is in intimate connection with the optic ganglia, and a [illegible] part

next to the first antennae.

The appendages (A.1. A.II. Md.) are all simple, but a bud now grows out from the under side of the second antennae, and gives them a biramous character. The one to the left of the figure is already bifid at the tip. Rudiments of the 1st pair of maxillae (Mx.I.) are also present. The mandibles very soon become bilobed, and the second antennae, the largest of the appendages, are then outstripped in length by the first pair. The ganglia of the antennae enter into the brain, while those of the mandibles form the first pair of the thoracic chain of ganglia, and are united to the brain by cords passing around the oesophagus.

The abdominal fold, at first vertical in position, now begins to grow forward and the anus A, which is situated at about the middle of its upper surface, passes anteriorly (i.e. backward in a morphological sense) until it comes to lie on the under side of the fold, near its tip. Somewhat later than this, a median groove appears at its extremity, which marks the notch of the telson plate, a still later acquisition. The mass of cells posterior to the anus, I interpret as the first trace of the hind gut (H). Large granular cells (Mo.) are seen on either side of the maxillae below the surface, while epithelium cells are freely sprinkled over the rest of the egg.

The section through the entire egg (Fig. 127.) will serve to orient us before passing on to examine the structure of the nauplius in detail. The abdomen is here out on a level with the arms and lies in a wide, shallow, depression. The yolk is composed of irregular blocks, only a few of which are represented, which abound in vacuoles, and scattered among them are numerous yolk cells, in all parts of the egg. Some of these ($y.c^2$) are settling down upon the ventral nervous system, while others (y.c y.c′) have wandered far and wide, through the yolk. The embryo is raised considerably above the general surface of the egg, but the chorion is probably more tensely stretched about it than represented. The second membrane is not shown in this drawing. In the longitudinal median section, Fig. 125., the comparatively large size of the abdomen is evident, also the short sternal region between it and the oesophagus, the relations of which have already been alluded to.

The labrum now becomes prominent (Lb.), as an outgrowth of ectoderm above the mouth. This section passes a little to one side of the anus, which occupies the position marked , . The brain or supra-oesophageal ganglion, has the appearance of compact ball (S.O.G).

Numerous [illegible](s) and circulating cells (. .) can be seen about the oesophagus, and vacuoliform yolk cells (y. c., y'.) may also be traced from the region of the abdomen to the surface immediately behind it. As in previous stages of development, the boundaries of surface cells are easily demonstrated, but this is not the case with the underlying elements. Very striking is the general character of nuclei or cells. As a rule the cell nucleus, or yolk cell is filled with small and large granules of chromatin, which stain deeply with haematoxylin.

The structure of this embryo is further illustrated by a series of 11 transverse sections (Fig .114,124), the first two of which cut the optic lobes and ganglia (O.L.), and the third passes through the anterior folds of the brain. (S.O.G.) The cells of the optic lobe, especially the outer tier, are large and columnar, and the smaller elements of the brain stain more deeply than those of the surface.

Between the lateral halves of the brain, there is a slight median depression (Fig. 116, M.E.) The three succeeding sections pass through the oesophagus (Fig. 117.), the 2nd antennae and mandibles (Fig. 118, 119.) In the first, the mesodermal cells (M.) entering the appendages from the yolk are very well shown,

also the [illegible] of spores and [illegible] cells, but the mesoplague. Some of the latter also occur within the appendage (Me., Fig. 118) On either side of the mesoplague there is a coarse reticulum of protoplasm (Ret, Fig. 117.), with wide meshes, free from cells or yolk particles. The yolk abounds in amoebic free granular elements. Some of them (Y.C.) are surrounded by protoplasmic processes, by which neighboring cells may be united, as shown under high powers (Fig. 33, Y.P.) They are usually however, separate, or at least no bond between distant cells can be detected. These bodies may be compared with amoebae and as already stated, they are found throughout the egg, but are most abundant above the embryo. The mandibular ganglion is sectioned in Fig. 118., where the median groove (M.G.) can also be ~~detected~~ seen. This is more noticeable in the next section, where the mandibles themselves are involved (Fig. 119. Numerous yolk cells (Me.) reach the ventral nervous system, investing it completely, and passing up the sides of the body, to form a thin layer, under the ectoderm (Ct., Fig. 116) These cells become spindle shaped and ultimately are converted into muscles and connective tissues. In Fig. 121, the ectoderm is still one cell thick on the middle line (M.L.), between the rudimentary maxillae, which are here

[illegible]. The tip of the abdomen shows the budding zone (B.Z.) of Reichenbach, which consists of a single tier of large granular cells. In the next section of the series, the small opening is [illegible] Fig.127.). The under concave face of the abdomen fits closely into the median furrow, and its dorsal, flat side, presses against the chorion.

The wall of the hind gut consists of a single layer of very large elements, and a slight lumen can be distinguished (F.12[illegible].) The ectoderm cells (Ect.) at the surface, have sharp boundaries, while the space between the intestine and body wall, is filled with loose masses of mesoderm which have not, as yet, a very definite arrangement. Some of these moreover (M.) are differentiated from the rest, by their small size, and greater staining capacity, and represent the rudimentary abdominal muscles.

The plane of section in Fig.123., is at the point of junction of the abdominal fold with the egg, while the next Fig.124., passes through the mass of cell (H.Fig.111.) behind the anus.

These are of mesodermic origin, that is they are yolk cells which migrated from the abdominal region. These wanderers (M[illegible]., Fig.124) have not yet reached their goal, and their route can be easily followed by a comparison with Fig.125.

The heart takes its origin in a central mass of cells. The yolk in the vicinity of the embryo is represented in many of the figures already referred to. It consists of corpuscles of various sizes, and of large blocks, containing vacuoles.

Some of these bodies (A.Y.S.) are granular and often have large lacunae in their interior, so that only a thin ring appears in the section. The chemical nature of the vitellus is further-altered, at the surface of the embryo, where it is broken down into small fragments, some of which stain lightly in haematoxylin. They resemble the spores but are colored much less intensely.

We now leave the egg nauplius with a rudimentary nervous system, consisting of two pairs of ganglia constituting the brain, in front of the oesophagus; with optic lobes or undeveloped eye-stalks, and at least, two pairs of post oral ganglia. There is an oesophagus,--a short tube closed in the side of the yolk, and a hind gut, opening by an anus, situated near the middle of the upper side of the abdomen, and communicating with the space filled by the vitellus. The mesoderm is differentiated, and the endoderm is represented by some of the cells lying in the yolk. There is no evidence of a histological or topographical nature, that any particular elements are destined from the first to give rise to the inner layer.

4.

SPORE and ENDOGENOUS CELL FORMATION.

Cell reproduction by spores plays so important a part in the early history of Alpheus, and besides, is a question of so much general interest, that it will be considered at some length.

I call the bodies in question " spores ", partly for lack of a better term, and also because this word seems to define them pretty accurately. They appear early in the 5th. phase, that is to say as soon as the naupliar appendages are outlined, in the region of the abdominal plate, and indeed generally, along the line of contact of the foodyolk with the embryo. Their numbers increase rapidly up to the fully developed egg nauplius, when they reach a maximum. They continue after this phase until 6--8, pairs of post oral appendages are budded off, when they disappear quite rapidly. It is worthy of notice, that by this time, a rudimentary vascular system is present.

What now is the origin of these bodies, and what becomes of them? I believe there can be but one answer to the first of these questions. They arise by endogenous growth from embryonic cells, chiefly as it will appear, from those yolk elements which migrate from the abdominal plate, and take part in forming the mesoderm.

Figs. 21 & 32 represent highly magnified portions of transverse sections of the egg-nauplius, corresponding nearly to Fig. 117., which shows the general relations.

In the first, the oesophagus (Std.) appears as a tube with conspicuous lumen. Its wall is composed of elongated irregular cells. It comes into close relation with the yolk above, while on either side there is a coarse reticulum of plasma (Ret.), connecting it with clusters of mesoderm cells, which lie near or within the pocket of the appendage. A granular residue of altered yolk lies near the oesophagus, while round about there are fragments of various sizes. Many of the larger blocks or spherules are vacuolated or otherwise changed, and here we find numbers of the spores in question.

These ( ) are quite small, highly refractive bodies, quite similar to the lumps of chromatin, which occur in contiguous cells, (Fig. 32, Mes.).

With care one may distinguish a clear hyaline body around the larger of these elements (Fig. 32, S'). The embryonic cells, whether mesoderm or ectoderm, are characterized by the presence of large nodular or stellate masses of chromatin. A single cell may contain one or several spore-like nodules.

A number of these are represented in Fig. 18, all of which are drawn to the same scale, and taken from the series under review, chiefly from the region of the oesophagus or abdomen.

It should be remembered that we are dealing with sections, and not in all cases with entire cells, which partially accounts for the variation both in the size and number of these bodies present in a given cell. The conclusion, that the balls of chromatin in cells d, f, g, etc, are the structures which we have called spores, when found free in the yolk, is unavoidable. The larger spore in cell f, for instance, is like cell b, with the exception that the latter has acquired a somatic layer of protoplasm. I therefore regard this body (cell b.) as a spore which was set free from the mother cell, and has in the course of growth acquired an outer, hyaline layer. The number of spores which may arise from a single cell probably varies, and depends upon the degree to which the division of the nucleus has been carried. In cell g, there is a swarm of granules of various sizes. The two spores beside cell k, probably do not pertain to that element. Sporulating cells of a similar and various character, may be seen by glancing over the drawings of the [illegible] nauplius and earlier phases, but it is hardly necessary to specify

to these again in detail.

The phenomena of endogenous cell formation do not appear to be confined to any layer or to any one special lot of elements. Probably all the cells in the egg are, ~~par~~potentially spore producers. The conditions which are most favorable ~~for~~ to this method of reproduction, may depend largely upon the nourishment of the individual cells. That a part at least of the superficial epithelium possesses this power, there is one very striking case in point, Fig. 36. At a later phase than the egg nauplius, when 6--8 pairs of appendages are present, there appears on the surface of the egg, very nearly opposite to that occupied by the embryo, a small patch of cells. This I interpret from its position as the possible remnant of a median, unpaired, dorsal organ, homologous to the structures which have been described under this name in various Arthropods. Beyond the fact of its occurrence and subsequent disappearance at this point, I cannot at present, say very much. Kingsley notices a similar structure in the embryo of Crangon, and his account up to a certain point, agrees perfectly with what I have seen in Alpheus.

A slight depression occurs in the centre of this area, and some of its cells (whether with or without a true infolding or

[illegible] , I am not able to say), multiply by endogenous division, producing an incredible number of spores, which pass down and into the yolk and are distributed through a considerable portion of the egg. The fate of this new army of recruits, I have not satisfactorily followed, but it seems possible at least, that they contribute, in part, to the mesodermic structures of the body.

The second question as to what becomes of the spores, is not easily answered, but there is evidence to show that some at least, are converted directly into blood corpuscles.

It is further probable, that others become ordinary mesoderm cells. In support of the latter view, we have the fact that these bodies are found in the lobes of the appendages, both of the egg nauplius, and of later stages. (Figs. 32, 118, S D′) Further, the number of spores produced, is much greater than the number of blood cells present at the time of the disappearance of the former.

On the other hand, the spore in course of its growth acquires the histological characters of the typical blood corpuscle. Several corpuscles from the blood of an adult Alpheus, are shown in Fig. 19., and others from an embryo of the same species in Fig. 35. B, C. They consist of a clear irregular body, with a deeply

staining granular nucleus, which conforms to its shape.

This last figure shows a part of one side, of a transverse section, from a well advanced embryo, in which the first traces of ocular pigment occurs. There is a stream of plasma (Pl.) at this time, which bathes the ventral nervous system, and passes up the sides of the animal, between the yolk and body wall.

Numerous blood corpuscles of characteristic appearance, are found in it, while there are other cells (Mc.) in the yolk, which probably supply the lateral somatic muscles (Ms.), and form a part of neurilemma, or connective tissue membrane over the ventral ganglia, between the plasma and vitellus.

The resemblance between the "spore"S' (Fig. 32.), or b. (Fig. 18.) both of which are true cells in the morphological sense, and the blood corpuscles just referred to, is quite striking, and is probably more than superficial.

Endogenous cell division may not be so rare an occurrence in the Arthropod group, as the meagre accounts which we at present possess on the subject, might lead us to suppose.

Reichenbach, so far as I am aware, is the only one who has given a detailed description of the process in crustacea, and his observations are not fully accepted.

The work of this excellent observer will be referred to presently. Most interesting in this connection, are the structures seen by Dallinger (18) in his study on the origin of the nucleus among the monads. He saw the mother cell or cyst burst, and pour forth a cloud of refringent spores, which could be seen, only with the highest powers. They are at first semi-opaque, but soon become hyaline, and strongly refractive. Each grows to become the nucleus of a new cell, but before the complete nuclear growth is attained, an outer cell body and flagella, are developed, the latter from the nucleus. In this case the extreme limit of nuclear division is perhaps reached, before the liberation of the spores. (V. Nelson's Significance of Sex, p. 28-29.)

Ishikawa (15) finds peculiar elements in the egg nauplius of the prawn Atyephira compressa, but does not trace their origin or function. They are "small granules" easily stained by logwood solution, and some are of considerable size and have a clear cell outline. "These are mostly aggregated in the cephalic region, between the involutions of the ectoderm cells, but are also found in all places". In time of appearance, and in their position, he says, they seem to correspond to the "secondary mesoderm cells" of Astacus. This short description with his figures show conclusively

that these bodies are directly comparable to the spores just described in Alpheus, and their history in both forms is probably the same. Fig. 62, of his paper shows a longitudinal median section through the nauplius embryo, and affords an interesting comparison with the similar phase of Alpheus.

It is evidently a trifle older than the egg represented in Figs. 100, 105, of this paper, but the general agreement between them is very marked, especially with respect to the character and position of the secondary mesoderm cells.

This author has clearly mistaken the abdominal cleft (marked P'.) for the proctodeum, which is formed behind the latter, and probably not at this stage. The wedge-shaped appearance of the cells of the abdominal fold, correspond exactly with those of Alpheus, and indicate in both cases a gradual crowding of these elements below the surface of the part.

Reichenbach, in his recent work on the development of the crayfish, pp. 36, 37, thus sums up his views upon the origin and function of the bodies which he calls "Sekundäre Mesodermzellen."

"Die fraglichen Elemente sind als Zellen zu deuten, deren Kerne nicht immer die Beschaffenheit gewöhnlicher Zellkerne haben, dieselbe aber früher oder später erlangen. (Fig. 20 [illegible] [2])

Sie nehmen ihren Ursprung innerhalb derjenigen Entodermzellen, welche die ventrale Wand des Ur[illegible]säckchens zu [illegible] durch eine näher zu erforschende Art endogener Zellbildung, bei welcher die in der Mehrzahl in den Elementen des Entoderms vorhandenen Kerne eine wichtige Rolle zu spielen scheinen.

In den dem Stadium D. vorangehenden Entwicklungsperioden hat jede Dotterzelle meist nur einen Kern; dies trifft auch noch zum Theil für Stadium D. zu. Bald vermehren sich aber die Entodermkerne ganz erheblich und endlich beginnen die sekundären Dotterzellen aufzutreten. Wenn eine grössere Zahl der sekundären Dotterzellen in den Entodermelementen liegen, so scheint das Kernmaterial verbraucht zu sein. Sie wandern mit aller Wahrscheinlichkeit nach diese Zellen, deren Kerne anscheinend noch in der Metamorphose sich befinden, aus dem Entoderm aus und begeben sich unter die Embryonalanlage. Die betreffenden Contouren des Entoderms lassen oft noch Spuren dieser Wanderung erkennen. Ob sie wirklich aktiv auswandern oder auch ausgestossen werden, ist nicht festzustellen gewesen. Sie begeben sich aus unter die älteren Dotterzellen und sind bald nicht mehr von ihnen zu unterscheiden. Aus diesem Grund führte ich für sie den Namen "sekundäre Dotterzellen" ein, während die älteren Dotterzellen

die primären bezeichnet wurden. Da sie in letzterer die Tendenz zeigen, zu kompakteren Massen zu verwachsen, so darf man wohl vermuten dass sie [illegible] zellen [illegible] Blutzellen [illegible] geworden.""

As already indicated these secondary mesoblast cells probably correspond, more or less directly, to the paracytes observed in Alpheus. In both forms they appear, and disappear at corresponding phases. In Astacus, for instance, Reichenbach first noticed them in stage D, (that is when the optic disks, the thoracic-abdominal process and the mandibles are outlined). They reach a maximum in the egg nauplius phase (Stage F.), and then speedily degenerate, being nearly absent in stage G., where 4 pairs of post-oral appendages are present.

In stage D., the cells in question are most abundant under the optic disks (Kopflappen), and in the region of the upper lip, but become more generally distributed in the egg nauplius. This agrees in general with what we have seen in Alpheus, remembering that the relations in the crayfish are altered by the fact that gastrulation appears after the optic disks are formed, and that the invagination instead of being solid, as in most prawns, forms an enclosed chamber within the yolk, and eventually gives rise to the mesenteron, or midgut of the adult.

This chamber is flattened out under the carapace, and the external yolk is gradually absorbed by the entoderm cells forming its wall, which grow to gigantic size in consequence. The nuclei of the latter lie at the peripheral ends of the cells, next the yolk, and these on the ventral side of the sac, opposite the embryo, give rise, according to Reichenbach, by endogenous cell division, to the secondary mesoderm.

Fig. 20, is a copy of Fig. 67, Plate 8, of Reichenbach's work, and is introduced here for comparison. It represents several entoderm cells of the ventral wall of the primitive digestive cavity, of the egg nauplius. These large columnar elements take up the yolk directly, grasping it by pseudopodia-like elongations of the cell, amoeboid fashion. They also contain granular protoplasm, vacuoles, and nuclear bodies, next to the vitellus.

Similar structures also occur outside the cells, in the yolk mass. These bodies are gorged with the abundant food, and may be compared, in view of their nutritive condition, with the swollen granular cells in the abdominal plate of Alpheus (V. Fig. 85 Y C).

Reichenbach's interpretation that the "sekundäre Mesodermzellen" found in the yolk, are in part derived from the entoderm cells, is probably the true one, and is readily supported from the observations above given.

The bodies n.′ in Fig.20., probably correspond to nuclei among the cells, f.c.n. (Fig 18) of Alpheus. In both cases they are deeply staining masses of chromatin, without external envelopes, while enclosed by the outer cells, but with a clear somatic portion, when free in the yolk. (Compare Fig. 20 K. [illegible] & Figs. 18 b, c 125. [illegible])

In Alpheus, the spore, when not free, does not generally possess a hyaline coat, so far as I can ascertain. This is pretty good evidence that these bodies are not taken into the endoderm cells along with the food yolk, as some have supposed, but that they are formed in these cells, and ~~pour~~ pass out into the vitellus.

I have seen nothing in the Alpheus corresponding exactly to the vesiculated elements described for the crayfish, and which may, but probably do not represent other structures, derived from the yolk. Fig 20, n. etc.

In the segmented egg of Astacus, certain anomalous bodies have been observed, which Reichenbach calls' "white yolk elements". "They consist of a protoplasmic, finegrained substance, and contain vacuolar inclusions, which give them a frothy appearance. They lie always just under the blastoderm, or at the center of the spherical egg, and disappear very soon".

In Fig. 30, (2[illegible]), one is drawn with a small nucleus ([illegible] [illegible] compressed), but this is not mentioned in the text, and may be accidental. Their origin and history is wholly unknown, but their distribution and general character lend some support to the view of Nusbaum, that they are converted into secondary mesoderm cells. He says (26) "Il est très probable que ces éléments, après avoir reçu leurs granulations brillantes, se transforment en cellules du mésoderme secondaire. Les cellules du mésoderme secondaire, une fois formées, émigrent dans le vitellus; comme les cellules entodermiques de l'Astacus fluviatilis dévorent le vitellus, il n'est pas étonnant qu'avec ce dernier passent aussi dans leur intérieur les cellules du mésoderme secondaire".

This seems plausible enough, but, for the reasons already given, there is no good ground for doubting the fact of endogenous cell division to account for a part, if not all, of these globules.

Nusbaum's general objection that he considers "une transformation d'un noyau en une cellule comme une absurdité histologique", has no weight in view of the facts which we already possess in the subject of cell reproduction.

Structures analogous to these "secondary mesoderm cells" have been observed in the eggs of insects, and Brauer (23) figures certain yolk cells undergoing endogenous division [illegible] beneath the blastoderm, in [illegible] embryos of [illegible] spider.

5.

COMPARISONS and GENERAL SUMMARY.

The literature of crustacean embryology has been so recently reviewed by several investigators in this field, (Reichenbach, Nussbaum, Kingsley.), that any discussion necessarily involves the repetition of much that has already been said.

Some points however, will be considered, upon which the observations of this paper bear most directly, such as the function of "yolk nuclei", the origin of germ layers and segmentation.

First in regard to segmentation, Alpheus belongs to the centrolecithal type, as defined by Balfour. The division of the yolk is delayed until the beginning of the 4th segmentation phase, that is until the appearance of 16. nuclei, with perinuclear protoplasm. Partial pyramids are then formed, which fuse in the common vitellus in the interior of the egg. This or a similar process seems to obtain with the majority of decapods, and with modifications, with Arthropods generally.

The type is clear enough, notwithstanding the minor secondary variations which different orders, and even species, may present.

Thus in Crangon (25) studied by Kingsley, the protoplasm reaches the surface of the egg before the 2nd phase of nuclear division is completed, and the furrows separating the yolk pyramids is practically absent. In Stenopus, according to my observations, the protoplasm travels to the surface very soon after the first phase of division. In one egg containing two nuclei, one of them was quite superficial, while the other was nearer the centre of the yolk. When the 3rd. phase of division is reached, the yolk is divided at the surface into 8 blastomeres, by deep furrows as in Penaeus, figured by Haeckel. Each nucleus is surrounded by perinuclear protoplasm, which is drawn out into a reticulum. The bases of the segments are very convex, giving the egg in surface view, exactly the appearance of a holoblastic ovum.

The septa between adjacent pyramids, are not marked in subsequent stages, and do not extend very far below the surface.

In Hippa talpoides, the first stages were not observed, but when about 64 pyramids are formed, the apices of them reach nearly to the centre of the egg. (Figs. 1 & 4)

In Palaemonetes vulgaris, I have obtained one stage with two nuclei in the centre of the undivided yolk, and another (Fig. 24) with about 32 yolk columns.

These sections recall Kingsley's figures of the egg of Crangon (No. 25. Pl. 1) Fig 4 , when the first nucleus has divided into 16, parts, most of which are at the surface. In Palaemonetes however, all products of segmentation reach the surface, which is not true of the other prawn.

The yolk in Crangon is not superficially divided, according to Kingsley. This may be an error of observation, as the fusion of the yolk spheres due to the action of reagents, or effects of imbedding , may easily obscure the relations present.

In Palaemonetes, delicate septa (Fig. 24. Sep.) which pass but a short way into the egg , separate adjacent segments. A large spherical nucleus (n) lies at the base of each of the latter. It is evenly granular and is surrounded by protoplasm, in contact with the surface of the egg. This is drawn out into very delicate, radial threads, which branch and anastomose in the yolk, and unite with the septa of the pyramid.

Mayer's study of Eupagurus shows another phase (5). In this prawn, 8 nuclei are found in the interior of the yolk, before the latter is affected. It then divides, not simultaneously into 8 pyramids, but like ordinary holoblastic ova into 2, 4, and 8 , blastomeres, which soon fuse in the interior, so that subsequent segmentation is superficial.

Asellus aquaticus, according to Ed. van Beneden and Balfour, resembles Gammarus except that the eggs divide only as far as 8. segments, or rather a similar number of nuclei are formed.

In Palaemon (3) the segmentation is regular, and at first total. But finally, the inner portions of each cell fuse to form a common yolk mass, exactly like that of the usual type.

A variation of another sort occurs in Callianassa subterranea where Mereschkowski (11) describes the blastoderm as forming in a somewhat peculiar manner. The first central nucleus divides into 16 parts, which travel to the surface, and form a peripheral layer of plasma enclosing the yolk. This gradually segments into 16 parts, corresponding to the number of nuclei present.

The segmentation is simultaneous over the egg, but the yolk, as in the case of insects, is not involved. These cells multiply without affecting the enclosed vitellus, and form a layer of tall prismatic elements. Then they become more numerous, flatten out, and decrease in size. There are no yolk nuclei.

The crayfish appears to be rather more peculiar in these respects. Notwithstanding the fact that this animal has been studied very thoroughly perhaps more completely than any other decapod, (by Rathke, Lereboullet, Bobretzky, Reichenbach, Ischikawa,)

any knowledge of the phenomena of [illegible].

[illegible] (16) finds that in the Galician crayfish (Astacus leptodactylus), the first nucleus with its plasma, goes to the surface of the egg, and there undergoes division. The nuclei which result from this process, (the exact number is not given) spread over the egg, and yolk segments are formed around them. At first the septa are superficial, but finally extend in, nearly to the center, which is occupied by a large spherical body containing yolk and oil droplets, the nature of which is not known.

Reichenbach (22) calls this the "Central Körper", and agrees with Schimkewitsch in considering it as a portion of the unsegmented yolk, but its fate has not been followed.

According to this observer, then, Astacus would be an example of the centrolecithal type in the most exact sense of the term.

We thus have all phases between a form like [illegible], where the segmentation is regular, and at first total, and involves at once the protoplasm and the yolk, and one like [illegible], where the deutoplasm undergoes no division whatever, or like [illegible], where it suffers but a very slight change, if any.

In some instances [illegible], and Alpheus, the yolk is divided only after a given number of nuclei are formed, 8 - 16, and then only partially.

Further, this [illegible] may [illegible] be replaced by a regular and gradual, or it may take place simultaneously around all the nuclei.

In the forms which I have studied no evidence of the first nuclei have left over in the yolk after the blastoderm is developed, unless we accept Alpheus minus, where this was not determined beyond a doubt.

Kingsley finds the same essentially true of Crangon. This is apparently the rule with decapods, although there may prove to be numerous exceptions. Atyephyra is an example in point according to Ishikawa (15) and it is to be noted that this species has a total and regular segmentation. He says ", Within the yolk-segments are a fair number of nuclei, placed not at the centre, but rather at one side of them. Each nucleus is furnished with a dark-staining nucleolus, and a layer of protoplasm prolonged into a reticulum. I have not traced the origin of these nuclear bodies, it is, however, probable that they are derived from the segmentation nuclei. In one or two of my sections I have [illegible] the [illegible] segmented into 128 parts".

This last remark indicates that these yolk-[illegible] [illegible] be supposed, and not directly from the blastoderm, as in Alpheus.

All the varieties of segmentation and blastoderm formation [illegible] above described are readily derivable from one like [illegible], and, as Mereschkowski observes, this may have been the primitive type. And further, it is not difficult to see again how from this the centrolecithal ova of such forms as Oniscus, [illegible], [illegible], could be derived. We would have this result immediately achieved in the crayfish for instance, if the protoplasm which migrated to the surface, should remain, and build up a germinal plate at one pole, instead of diffusing itself over the egg.

On the subject of Arthropod segmentation Kingsley (25) says "The protoplasm segments, the yolk in most hexapods and some crustaceans does not, but this yolk in either group is to be regarded as superficial rather than central, and the term centrolecithal, though not necessary, is far preferable to endo- or ecto-lecithal. The nuclei, and the surrounding protoplasm are clearly to be regarded as cells." The segmentation of the yolk [illegible] the yolk itself, is a secondary feature. The question of terminology in this case does not seem to be important, inasmuch as there are all varieties of this type. Whether the protoplasm lies at the centre of the egg at first, or not, a centrolecithal condition is eventually attained. Balfour recognized this in his definition of the term.

He says: "As might be anticipated on the analogy of the types of segmentation already described, the concentration of the food yolk at the centre of the ovum does not always take place before segmentation, but is sometimes deferred till even the later stages of this process".

The question as to whether the first ~~phases~~ products of segmentation are to be considered cells or not involves merely a definition of terms. In a physiological sense all independent masses of chromatin are potentially cells. The undifferentiated chromatin is the essential, and the surrounding plasma and membranes, are the secondary and incidental ~~characters~~ structures. The spore starts as a simple mass of this peculiar substance, derived by division from a larger mass or nucleus, and becomes the nucleus of a new cell, surrounding itself with protecting membranes of its own make. The chromatin or nuclein which is reserved for reproduction, may sever itself, according to its needs, with 2, or 3, or perhaps more concentric envelopes. It is no more of a cell however, in the fundamental sense, than it was before.

From the morphological point of view, on the other hand, we recognize various stadia in the development of cells. In the first place we may regard the whole mass with its nucleus, perhaps less

protoplasm or cytoplasm, with its differentiated products (outer membrane, if it have any), and the formative cytoplasm, as constituting the cell in the morphological sense.

Then logically we have a syncytium in the [illegible] of Alpheus [illegible], when 8 nuclei are formed before segmentation affects the yolk, and we have two cells in Palaemon or Atyephyra, when the whole egg or morphological unit divides into two parts, or we have 16 cells in Alpheus, when the first yolk pyramid stage is attained. In this case the cells open by their central ends into the common yolk mass. By continued division of the pyramids, we get ultimately the superficial cells of the blastoderm, or of the embryo, containing only the nucleus and protoplasm at its peripheral end, while it is in contact with the yolk below. The cells which are included in the yolk at the gastrula phase, or which are crowded below the surface at a later period, are units of the same kind, although their cell boundaries may be lost. The elements which pass into the yolk to take part in the mesoderm or endoderm, may lose their outer plasma, and be degraded to nuclei in one sense, but raised to the dignity of cells in the higher functional sense, as shown by their powers of reproduction.

Again, from a physiological standpoint, we may regard the segmentation nucleus with its perinuclear reticulum as the cell or unit, and its products, which appear to have the latent powers of amoebae, as cells without definite boundaries.

The yolk is evidently a secondary acquisition, but the segmentation of this about the nuclei and protoplasm, must be due merely to the inherited tendency of the cytoplasm of the whole cell to take part in the division started by the nucleus.

We may have, of course, not only amoeboid cells, but amoeboid nuclei or nucleoli or spheres, and we may regard these functionally, as units of equal value.

In the previous observations the various elements of the egg and embryo are generally referred to in the morphological sense, but there need be no confusion, even if this rule is not strictly adhered to.

The origin and function of yolk 'nuclei' in general is a subject on which new observations are greatly needed. It is without much doubt true that all the chromatin elements of all eggs are derived from the first nucleus, and that the apparent spontaneity in origin of such bodies, is due to imperfect knowledge.

By "yolk nuclei" or "yolk" cells are here meant those bodies

which appear in the deutoplasm before the germinal layers are formed, often simultaneously with the blastoderm.

Nusbaum (26) concludes that "they take no part in the formation of the endoderm, the muscles and other complicated mesodermic organs, but serve for the absorption and solidification of the yolk, as well as in part at least, for the formation of the blastoderm". He regards the secondary mesoderm cells of Astacus in this light. We have shown that Reichenbach's interpretation of the origin and function of these structures is more probably the correct one, and the spores of Alpheus, whether analogous or not to "secondary mesoderm", certainly do not fall into this category. In fact there are no bodies in the egg of this prawn which fulfil the conditions above given. The cells which migrate from the blastoderm into the yolk become indistinguishable from those which join them at gastrulation, and all appear to take part in forming tissue.

These first migratory yolk cells may give rise in part, to the endoderm, as might be predicted from the general functions of this layer, but exactly what this part is I am unable to determine.

The germ layers of Phryganids (Neophalax) (13) are shown by Patten's studies to present some interesting analogies with what has been observed in Alpheus. The morphological value of these similarities is probably not great, yet they point to the fact that the significance of the germinal layers in the early stages of certain Arthropods, has been profoundly modified.

In Neophalax as in Alpheus all the segmentation nuclei take part in forming the blastoderm, which becomes thickened at one pole, and gives rise to a ventral plate. A protoplasmic layer or blastema is present in this insect egg, as in the egg of the spider. Yolk cells or "endoderm" arise "from any point in the blastoderm by delamination, and this process may continue even after the blastoderm has been converted into the ventral plate". Patten states that the greater part of these "yolk cells" ultimately give rise to the epithelium of the mid gut, and hence are true endoderm. This is analogous to the migration of blastodermic cells, which take place in the prawn, only I have not been able to trace with certainty their ultimate fate, and in this case I had no actual proof of delamination by karyokinetic figures, although dividing cells both at the surface and in the yolk were commonly met with.

That some of the blastoderm cells migrate at once into the vitellus, before splitting, is abundantly shown by the figures illustrating this phase. (Figs. 37--45.)

A further point of resemblance is that at gastrulation both mesoderm and yolk cells are formed. The latter, however, do not appear at once. " After the segmentation of the mesoderm, certain cells are observed in stages of separation from the mesodermic segments, which probably migrate into the yolk, and then cannot be distinguished from the ordinary yolk cells ".

The yolk cells of Oniscus were derived by Bobretzky (1) from the germinal eminence, but their function is not, according to Nusbaum (26), to form the endoderm, but to digest the yolk.

In spiders (Agelaena), Locy (20) finds the "yolk nuclei" to be products of the first nucleus, which are left over in the yolk, and never reach the surface. They multiply and are very numerous at the time of hatching.

Balfour (7) found similar nuclei, which he thinks not only form the walls of the hepatic ceca, but also that they are continually being added to the mesoblastic plate.

In insects there is probably considerable variety in the origin of these structures.

Bruce (23) concludes that in Thyridopteryx(Lepidopter) the yolk cells are undifferentiated products of the segmentation nucleus which have not reached the surface. As just seen, Patten finds the reverse true in Phryganids.

Accordingly it appears that yolk cells, in Arthropods at least, are derived either (a) directly from the first nucleus, and may never reach the surface, or (b) from the blastoderm.

Their function is not in all cases clear, but is probably various. They may or may not take part in forming tissue, or may act as yolk digesters, whether serving another function or not.

As regards the origin of the inner germinal layers, the observations given in this paper are not altogether in agreement with the commonly accepted views.

The mesoderm in Alpheus has probably a composite origin. It is partially due to cells budded off from the lateral and anterior border of the gastrula depression. Some of these migrate into the yolk and thence by a circuitous path wander to the anterior parts of the embryo. They may multiply endogenously giving rise to spores which subsequently play the part of mesoderm cells. The cell mass forming the abdominal plate continues to receive recruits from the surface ectoderm for a considerable

period after the blastopore is obscured.

Ectoderm cells on the surface of the egg multiply endogenously, and send spores into the yolk, which without much doubt, are mesodermic in function. It seems hardly probable that these bodies would be formed, and then forthwith absorbed.

The endoderm arises from certain of the yolk cells, but as these have various sources, and are not histologically different, it is not possible to trace their primary origin with certainty. This inquiry may really be unimportant, since there are reasons for believing that all the cells in the yolk are, up to a certain period, unspecialized.

Kingsley's account of the process of gastrulation in Crangon (25) is much simpler, but this may be partly owing to the fact that his material was incomplete. (In this connection compare his Fig. 9. Pl. 1 with Figs. 49, 55) According to this observer, the invaginated endoderm cells pass vertically into the yolk as a solid mass. This subsequently divides, one portion going to the region of the stomodaeum, while the other does not greatly change its position. Later, both unite, join the proctodaeum, and form the midgut. "Through all of the larval stages the endodermal cells can be readily recognized from the fact that their

nuclei stain less deeply than those of mesodermal or ectodermal origin". His account of the origin of mesoderm is less definite. It arises, he says, either wholly or in part, from the lateral and anterior sides of the blastopore. He saw nothing that looked like budding of mesoderm cells from either ectoderm or endoderm.

In Astacus (22.) the conditions are altered by the character of the gastrula. Here a considerable area of superficial cells is invaginated in the form of a circular plate. But before this happens, the optic discs have made their appearance, and also the rudiments of the thoracic-abdominal process.

At this time (Stage A. of Reichenbach) the mesoderm is represented by large cells below the surface just in front of the endoderm plate, that is, at the anterior border of the future wall of the gastrula cavity. They must evidently arise by active division of the ectoderm at that point, but Reichenbach does not determine their origin with certainty. After invagination the mesoderm occupies the space between the ectoderm and the anterior wall of the gastrula. Thus, to this effect, he says-- "die Elemente des mittleren Keimblattes an der Ubergangstelle des aussern in das innere Blatt am vorderen Urmundrande ihrer

Ursprung nehmen. Aller Wahrscheinlichkeit nach liegen seine Urzellen früher in der Kugeloberfläche der Blastosphaer und gelangen durch Abschnürung und lebhafte Proliferation in der fraglichen Region in die Tiefe, wo sie sich bald vermehren und durch Wanderung verbreiten, um die Bestandteile des Mesoderm den verschiedenen Embryonalregionen zuzuführen". (No. 22, p. 18.)

In stage F, when the rudiments of the mandibles are formed, the secondary mesoderm cells have appeared. The middle layer is more extensive, and its elements do not sink into the yolk, but keep close to the ectoderm. It assumes greater and greater proportions, and in the egg nauplius phase shows traces of segmentation. It extends forward from the anterior wall of the primitive digestive cavity and is bilaterally symmetrical with respect to the long axis of the embryo. Here as in Alpheus, the mesoderm has not a simple origin, and the analogy between the secondary mesoderm cells and spores has already been shown.

The comparison between the primary mesoderm, which is probably derived from superficial cells before gastrulation, and the elements composing the abdominal plate of Alpheus is less obvious. Of course the relations of the yolk to the endoderm in the two forms is reversed.

According to Bobretzky (3) the endoderm or hypoblast in Palaemon, which is derived from the bottom of the gastrula cavity, multiplies in the yolk, and quite fills it. The vitellus undergoes a secondary segmentation, into a great mass of "yolk cells" with large nuclei, at first distinctly, but later indistinctly separated from each other. These, represent the endoderm. The mesoblast is supposed to arise as already described in Crangon. In Atyephyra, Ishi Kawa (15) concludes, on not very clear evidence, that the endoderm is derived from the invaginated cells which ~~pour~~ pass into the interior of the yolk at the gastrula phase, and become indistinguishable from the nuclei already present. The mesoderm is derived from the anterior side as well as from the bottom of the cavity of the gastrula. There is every reason to believe, as already stated, that the secondary mesoderm, which he describes, are spores, not unlike those which occur in Alpheus.

Of Eupagurus, Mayer (5) states that the mesoderm arises from the upper cells of the anterior half of the gastrula, considered as ectoderm, and thence extends forwards. The endoderm originates from the bottom of the gastrula, and appears later as "nuclei" in the yolk.

The early stages of Mysis chameleo, recently studied by Nusbaum (26), present some points of interest. The segmentation is meroblastic, as in Oniscus. In the youngest stage he found, there was a circular, blastodermic disc. The egg is surrounded by a delicate homogeneous membrane (probably the chorion). The disc spreads, and forms a delicate blastodermic layer over the whole surface. This is very thin on the dorsal and lateral parts, but on the ventral side it is thickened. The disc now divides into three parts, an unpaired median and two lateral portions. The lateral thickenings represent the primitive ventral bands. These grow forward, making an obtuse angle with the median unpaired process, which is the rudiment of the abdomen.

Their enlarged ends represent the optic thickenings, and the nauplian appendages soon make their appearance along these bands.

The disc when first seen, consists of fine granular protoplasm, and has a large nucleus, the segmentation nucleus, imbedded in it.

In the 3rd. stage observed, the formative plasm has become differentiated into two layers, an outer striated one in which only one nucleus was observed, and an inner granular stratum.

The single external nucleus divides and gives rise to a small blastodermic disc, composed of a single layer of hexagonal cells.

Further,the nuclei and protoplasm of the inner layer give rise to a small mass of cells,and also receive accessions from the disc. The caudal plate,which is developed from the middle part of the latter,is composed of several layers of cells and is ~~covered~~ crossed by a transverse furrow. The cells below this furrow,are the products of the division of superficial cells. They divide energetically and most of them sink into the yolk,and probably take no part in forming the endoderm. The endoderm: " appears to arise independently from a definite part of the blastoderm,when the latter surrounds the whole egg."

" Le mésoderme se développe sur toute la longueur de deux moitiés épaissies de la bandelette ventrale,-entre le disque caudal et les elargissements antérieurs,que nous avons appeles optiques" . "Les cellules mesodermiques se forment par la division des cellules de l'ectoderme primitif dans la direction transversale et longitudinale (c'est -a -dire tangenté ou rayonnée), ou encore directement,par les cellules ectodermiques totales,qui s'enfoncent sous forme de coin au-dessous du feuillet externe" .

Les cellules du mesoderme se trouvent exclusivement au-dessous du bord epaissi de la bandelette ventrale.

Ainsi le mésoderme a une origine paire et se forme par la division des cellules ectodermiques sur les bords épaissis de la bandelette ventrale".

In the nauplius phase the mesoderm forms three paired masses, or solid segments. The yolk cells which migrate from the ventral plate,absorb the deutoplasm,and appear to alter its chemical nature,and finally to dissolve. We thus have eventually in Mysis what obtains in decapods generally, although the original process is altered by the great secondary change which the gastrula has undergone in this case.

In certain insects,the invaginated ectoderm is separated off to form the mesoderm.(23,) This rudiment then splits into two bands along the line of the "blastopore".After this solid somites are formed. In regard to the origin of endoderm there is less agreement among observers,but the cells remaining in the yolk, generally take a more or less important part in this layer.

Arachnids resemble insects in respect to formation of mesoderm. The first trace of the embryo,or primitive cumulus,is formed in Agelaena (20) from the blastema and the products of the first nucleus. The latter migrate from the interior to the surface of the egg,and join the blastema or protoplasmic cup.

The cumulus may appear before (23), or after the blastoderm. The mesoderm is derived from cells of the cumulus. It takes the form of two bands, which segment into the somites. According to Balfour (7), this layer also receives accession from the yolk cells. In Julus terrestris there are many resemblances to spiders in the early stages. Heathcote (12) finds in the yolk of this myriapod, nuclei, which he supposes to represent endoderm. A keel or ventral plate is formed, similar to the cumulus of arachnids, and recalls the blastodermic disc of Mysis and the germinal eminence of Isopods (Oniscus (1) Cymothoa (6)). It is due to a thickening of the blastoderm at a given point, and to yolk cells, which migrate thither, from the interior.

This author speaks of the blastoderm as the "ectoderm", which confuses his account. The mesoderm is formed from the keel, and splits into two layers, which grow around the yolk, and later become differentiated into two bands. These are afterwards const~~itu~~ricted into solid somites.

In Peripatus capensis the relations are considerably altered. Segmentation is complete but unequal; the blastopore persists, according to Sedgwick (17) and gives rise to the mouth and anus. The gastrula mouth enlarges in the direction of the long axis of the

embryo, ~~thus becoming epibolic~~, and the cavity of invagination gives rise to the mesenteron. The primitive streak develops behind the blastopore, and is due to the growth of indifferent cells. The mesoderm grows forward from the cell mass "as two ventro-lateral bands, one on each side of the blastopore".

We thus have in certain crustacea (Schizopods, Isopods) in Myriapods (Iulus), in spiders, and probably also Limulus, (14) a mass of embryonic cells called by various names, which in all cases represent the first trace of the embryo. It is derived either from the nucleus and formative protoplasm which separates at once from the yolk, or from the products of the nucleus, which migrate to a given point at the surface (in some cases to a blastema), either before or after a blastoderm is formed.

The mesoderm, in whole or in part, originates in a similar manner in all these forms and splits into two bands, which are usually at once divided up into somites. There is less similarity in the origin of endoderm, since this depends largely upon the disposition and relations of the food yolk. It is probable that in all those cases, as well as in Tracheates, we have to do with a modified gastrula.

The Arthropods show pretty general agreement in the formation

of the stromadaeum and proctodaeum. In Isopods the stomodaeum (with some exceptions, perhaps) appears in front of the blastopore and before the invagination of the hind-gut. In Tracheates (23) the stomodaeum is also formed first. This is true of Myriapods (Iulus), and Arachnids (20).

While in gastrulation, and in the development of mesoderm, and the formation of the oesophageal and anal invaginations, there are these striking similarities, yet many of them may be unimportant, and in establishing relationships, all characters both embryonic and adult must of course be considered. As Balfour pointed out, the Tracheates seem to occupy middle ground between the Crustacea on the one hand, and the Arachnids on the other.
The relations of Peripatus to the Arthropod phylum are not yet clearly made out.

SUMMARY.

1

In the ovary of Alpheus the germogen lies on the median lateral side of each ovarian lobe, while in Homarus it occupies the central, axial portion, and in Palinurus there is a germogen for each compartment of the ovary. The ovum originates in Homarus and Palinurus from nuclei which are imbedded in a common ovarian tissue. In some decapods, possibly in Alpheus, each egg arises from a distinct follicular cell, with nucleus and body wall.

The number of germinal dots varies with different genera. In Homarus there is a single one, placed always at the periphery of the vesicle, while in both Alpheus and Palinurus there are several.

A zone of coagulable matter is soon differentiated about the nucleus, which is destined to become the germinal vesicle of the egg (Homarus), and represents the rudimentary yolk.

A single layer of epithelium is organized about this, and becomes the egg follicle. Between this yolk and follicular wall a chitenous membrane, the future chorion, appears in ovarian eggs, ~~doubtless~~ a secretion product of the follicle cells.

In the mature ovum the vesicle is metamorphosed, or at least becomes invisible under the usual conditions, but reappears after the egg is laid, even if fertilization is not effected.

The fertilized egg is enveloped by a single membrane, the chorion, or shell, which closely invests the yolk.

2. In Alpheus minus, segmentation is direct and at first does not involve the deutoplasm. There results, by a kind of free cell formation, or endogenous division, several large cells or spheres, which are distributed evenly through the egg, and about them the yolk segments. The septa between the blastomeres may pass deep into the vitellus. Before a blastoderm is formed the egg is filled with large granular nuclei, which are undoubtedly descended, more or less distinctly, from the spheres just mentioned.

3. In all other species of Alpheus studied, the first nucleus undergoes a spindle metamorphosis in the centre of the egg. Each product consists of a large granular nucleus, with perinuclear protoplasm, which is drawn out into ray-like processes. These elements pass outward, impelled probably by a centrifugal force, (assisted possibly by amoeboid locomotion), and in the 4th. segmentation phase, when 16. nuclei are formed, the yolk divides superficially around each, to form pyramids. The apices of the blastomeres do not reach the centre of the egg, which is occupied

[illegible] segmented [illegible], the [illegible] and may ultimately [illegible] taken below the surface.

4

In [illegible] the formation of segmentation [illegible] as in Alpheus, in Stenopus hispidus, sp. (?) when 8 nuclei are formed, the vitel[illegible] at the surface by [illegible], into the [illegible]. In Palaemonetes and Hippa [illegible] the yolk [illegible] central [illegible] cally-limited modifications. The segmentation of all these eggs, including Alpheus, is at first in the interior of the egg, but eventually in the yolk, a centrolecithal condition being attained.

5.

The yolk cells or pyramids multiply by geometrical progression, and for a time their number increases ~~proportionately~~ while ~~ratio as~~ the size of the cells is proportionately diminished. The egg is radially symmetrical. Cell division soon becomes localized at a part of the hemisphere of the egg, while [illegible] in [illegible] shed off. The germ [illegible] rapidly [illegible], [illegible], [illegible] of a simple layer of cells, invest the egg. The blastoderm [illegible] nuclei, and [illegible] the yolk, [illegible] of the yolk, which [illegible] all the [illegible] egg. It is [illegible] directly [illegible] from the yolk pyramids, [illegible] topographically [illegible] with it.

Cell [illegible] early part of the [illegible] the [illegible] a germinal [illegible] formed, and [illegible] the [illegible] of the [illegible]. These [illegible] are indistinguishable from those yolk nuclei which appear during and after the gastrula phase.

6. Gastrulation takes place at the hind end of the germinal area, and involves comparatively few of the surface cells. The cavity is slight and soon disappears. The long axis of the future embryo can now be laid off. It passes through the blastopore, and the middle of the germinal area [illegible] to it. Cells [illegible] the gastrula cavity, and [illegible] pass into the yolk, and [illegible] migrate from the [illegible] the point of the original blastopore, [illegible] just [illegible]. A [illegible] plate is formed called the [illegible] plate or [illegible] the yolk-blastoporal [illegible]. By the growth of this plate, the [illegible] of the blastopore region appears to be [illegible]. Elements pass from it to all parts of the egg.

7. The sources of yolk nuclei is 3 fold:-

(1) From the blastoderm,
(2) from the gastrula and [illegible] in the region of the blastopore after its closure,
(3) from the dorsal surface of the [illegible] at [illegible] stage.

These [illegible]. The majority [illegible].

[illegible] gut. [illegible] the yolk [illegible] [illegible] -

[illegible], [illegible] which later by a growth [illegible] move through the yolk, and become specialized [illegible] [illegible], like the [illegible]. Some reach the periphery of the egg, and form vitelline epithelium. Many other yolk cells [illegible], and give rise to the endodermal structures, (mid-gut, liver).

The [illegible] cells appear to be specialized from the start, [illegible] the yolk [illegible].

The [illegible] [illegible] the yolk cells and [illegible], [illegible].

The vitelline [illegible] of the yolk [illegible].

8

[illegible] cell-dividing stage [illegible] in the early stages. [illegible] and yolk [illegible] in this way. [illegible], just before [illegible]. They [illegible] all parts of the [illegible] the yolk, and [illegible] of the [illegible], [illegible] of the [illegible]. They reach [illegible] the [illegible], and [illegible] 6-8 [illegible]. [illegible] arranged [illegible].

[illegible].

9

[illegible] is [illegible] in front of the [illegible] mouth, and [illegible] of the [illegible] part of [illegible]. It [illegible] with [illegible] by [illegible] cell [illegible]. The [illegible], and [illegible] probably [illegible] to the right, [illegible] with [illegible] of the [illegible], [illegible] in [illegible]. It [illegible] ly [illegible] the [illegible], to the right.

10.

The optic [illegible] are [illegible],

as a [illegible] of the [illegible] as the [illegible].

The [illegible] is brought about ;(1) [illegible]

(2) by [illegible] of cells from the [illegible], [illegible].

[illegible] they [illegible] their [illegible].

[illegible] of the [illegible] is [illegible].

11.

The heart [illegible]. It is [illegible], [illegible].

The [illegible] inal [illegible], [illegible] lum.

12. [illegible] of secondary convolutions.

The embryo [illegible] early stage, [illegible] however, relatively large [illegible] slightly [illegible].

An [illegible] of the embryo has [illegible] results. [illegible]

(1) Bobretzky, N.

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A. Anus.

[illegible]$^{1-6}$ Blastoderm and yolkcells.

A.1 First antenna.

A.(11) Second antenna.

Ab. Abdomen.

Ab.C. Abdominal cleft.

Ab.P. Abdominal plate.

Al.C. Alimentary canal.

Ap. Appendage.

A.Y.B. Altered yolk.

[illegible]$^{1-5}$ Invaginate [illegible] of gastrula.

B.C.,B.C.' Bloodcorpuscle

Bl.C. Blastoderm cell.

Bl.S. Blood sinus.

Bp. Blastopore

B.S. Blood space.

B.Z. Budding zone.

Ch. Chorion.

C.M. Area of invagination in [illegible] disc.

E.P. External process of yolk cell.

Ch.W. Chitinous wall of ovary.

C.T. Connective tissue stroma of ovary.

D.A. Dorsal aorta.

e, e,$^{1-2}$ Ovarian eggs of Alpheus.

ec., ec.$^{1-3}$ Ectodermic cells.

Ect. Ectoderm.

Ep., Ep.' Epiblast.

F.C. Follicular cell.

F.E., F.E.' Follicular epithelium.

G.D. Germinal disc.

Ger., Ger.^{2} Germogen.

G.V. Germinal vesicle.

H. Heart.

Hg. Hind-gut.

i. Secondary mesoderm cell. (endodermal nucleus)

I.C. Invaginate cells of gastrula.

I.E. Undifferentiated epithelium of ovarian follicles.

k. k' 1. Secondary mesoderm cells.

Lb. Labrum.

[illegible]	[illegible]	[illegible]	Primitive [illegible].
[illegible] 1-3	secondary [illegible] cells.	[illegible]	Perinuclear [illegible].
[illegible]	[illegible] of yolky [illegible].	P.Y.C.	Primary yolk cells.
[illegible]	[illegible]	Pot.	[illegible]
[illegible]	[illegible]	S.S'	Spores.
[illegible]	[illegible]	S 1-5	Spore-bearing cells.
[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Mouth.	S.O.G	Brain or Supraoesophageal ganglion.
Mu.	Muscle.		Swarm of spores.
Mx. (1)	First maxilla.	St.A.	Sternal [illegible].
N'	Nucleus.	Std.	Stomodaeum.
[illegible]	Nucleoli.	W	Outer wall of yolk pyramid.
O.E.	Ovarian egg of lobster.	Y.C'	[illegible] secondary yolk cells.
[illegible]	[illegible]	T.[illegible]	Transverse [illegible].
		V.[illegible]	Vacuole of [illegible].
[illegible]	[illegible] ganglion.	Vit	Vitellogen.
[illegible]	[illegible]	X.	Nucleus of 3rd segmentation phase.
[illegible]	Oil drops.	Y.	Yolk.
[illegible]	[illegible]	Y.B.	Yolk [illegible].
[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	Y.P.	Yolk pyramid.
[illegible]	[illegible]		Yolk spherule.

PLATE. 1.

Fig. 1

Surfaceview of egg of Hippa talpoides, with about 32. segments of yolk pyramids.

Fig. 2

Surface view of egg of Hippa talpoides, showing the optic discs, and abdominal plate of the early embryo.

Fig. 3

Transverse section through the germogen, or central axis of ovarian lobe of the Lobster.

Fig. 4

Section through an egg of Hippa talpoides, of about the age represented by Fig. 1.

Fig. 5

Part of a section of the segmenting egg of Alpheus minus, showing one of the yolk cells.

Fig. 6

Section similar to that shown in Fig. 3, but drawn with a lower power. The diameter of the entire ovary is twice that of the section.

Figs. 7-8.

Surface views of egg, nauplius, and later embryo of Hippa talpoides.

PLATE 2.

Fig. 9

Section of egg of Alpheus, with 8 nuclei present, but yolk unsegmented.

Fig. 10.

Surface view of similar egg, with 16 nuclei, and yolk superficially segmented about each in the form of pyramids.

Fig. 11

Section through the ovary of Alpheus.

Fig. 12.

Section through segmenting egg of Alpheus minus showing the spore-masses.

Fig. 13

A single spore-mass or sphere, enlarged.

Fig. 14

Section through egg of A. minus, showing first nucleus, about to divide.

PLATE 3

Fig. 15

Section of egg of Alpheus, with about 64 yolk pyramids present.

Fig. 16

First nucleus, before segmentation.

Fig. 17

Section of infertile egg of Alpheus, 5 hours old.

Fig. 18

Spores and sporulating cells, taken from different parts of the egg-nauplius embryo.

Fig. 19

Adult blood-corpuscles.

Fig. 20

Endoderm cells from the ventral wall of the primitive digestive cavity of Astacus fluviatilis (egg-nauplius stage) to show the origin of the secondary mesoderm cells. The latter lie both within and without the endoderm cells and appear to be in various stages of their metamorphosis. Copied from Reichenbach (22) Taf. VIII. Fig. 67.

Fig. 21

Portion of transverse section through egg-nauplius in region of oesophagus. Several spores are met with, some with the character of blood-cells.

PLATE 4.

Figs. 22, 23.

Swollen elements from the egg of Alpheus minus.

Fig. 24.

Section of egg of Palaemonetes vulgaris, showing the nucleus and the base of a yolk pyramid.

Figs. 25, 26.

Sporulating cells from egg of A. minus.

Fig. 27.

Section of egg of Pontonia domestica, before segmentation of yolk: 4, separate nuclei and two in process of division. One of the latter is in the last phase of karyokinesis.

Fig. 28.

Nucleus of egg of Alpheus of same stage as Fig. 9, in karyokinesis.

Fig. 29.

Section of egg of A. minus, before the blastoderm is defined.

Fig. 30.

Nucleus X, Fig. 9., greatly enlarged.

Plate. 5.   Plate. 5.   Plate. 5.

Fig. 31

Section of the yolk pyramids of Alpheus of the same phase as that shown in Fig. 15.

Fig. 32

Portion of transverse section of egg nauplius, to illustrate endogenous cell division.

Fig. 33

Cells in yolk above the same embryo.

Fig. 34

Part of section through similar embryo of another species, to show yolk cells which migrate to the surface, and become transformed into epithelium.

Fig. 35, Part of transverse section of embryo with eye pigment forming to show blood corpuscles.

Fig. 36.

Portion of longitudinal section, opposite embryo, of a phase with 4--6 post naupliar appendages, to show spare divisions of superficial cells.

Plate. 6.

Fig. 37.

Part of section of egg before gastrulation.

Figs. 38--44.

Consecutive sections of same egg, to show migration of cells of blastoderm into the yolk.

Fig. 45.

Section through same egg, drawn with more detail.

Fig. 46.

Section of egg of another species, in similar stage.

Fig. 47.

Surface view of germinal disc of the egg illustrated by Figs. 37--45.

Fig. 48.

Tangential section of same egg.

PLATE. 7.

Figs. 49--55.

Series of transverse sections of the gastrula.

Fig. 55, the most anterior, cuts the germinal disc (G.D.)

Fig. 50, 51. are drawn with a higher power to give the details.

PLATE 8

Fig. 57.

Section through the egg and germinal disc, just prior to gastrulation; 20½ hours older than the yolk pyramid phase represented in Fig. 15.

Figs. 58, 59, 60.

Longitudinal sections through the embryo. The section in Fig. 59 is nearly median.

PLATE 9.

Figs. 61 62 68 69

Transverse sections through egg shown in Fig. 58.

Fig. 63

Portion of median longitudinal section of same egg, greatly magnified.

Figs. 64-67.

Consecutive transverse sections of left optic disc of the same.

PLATE 10.

Fig. 72.

Surface view of embryo and egg.

Optic discs more than one cell thick, and united by cords of cells to abdominal plate (Ab.P.)

Figs. 70-71, 73, 74 & 75 (Plate 11.)

Series of longitudinal sections through the embryo.

PLATE 11.

Fig. 75

Median longitudinal section of embryo represented in Fig. 72.

Figs. 76-83

Consecutive transverse sections of left optic disc of same, of which Fig. 83, is the most posterior, and cuts the region of the first antenna. These show the first step in the thickening of the disc, by migration of cells from the surface.

Fig. 84

Transverse section through the optic disc, and entire egg.

Fig. 85.

Transverse section of the abdominal plate, in front of the primitive mouth, which has disappeared. This shows cells migrating from the surface at this point.

PLATE 12.

Figs. 85-90.

Longitudinal sections through an embryo somewhat older than that shown in Fig. 72. The rudiments of the appendages appear, and in Fig. 90 the optic disc (O.D.) is cut.

Fig. 86

Longitudinal section through the optic disc of an egg 6 hours older, from the same female.

Fig. 87

From the same egg, involving the inner border of the optic disc, and the outer edge of the abdominal plate. Yolk cells are here seen, as in the previous figures, migrating to all parts of the embryo and egg.

Fig. 91.

From an egg 12 hours older, from the same female. Transverse section through optic disc and egg. These are now united by a solid cord (.C), and have increased considerably in thickness. Some wandering cells (Y.C.) have reached the extra-embryonic surface of the egg.

PLATE 13.

Fig 93

Surface view of embryo with rudiments of 3 pairs of appendages. The external face is covered by a single layer of cells.

The oesophagus and abdominal fold have not yet appeared.

The area of multipolar invagination or thickening of the optic discs, is marked by large, granular cells. (C.M.)

Figs. 92-94, 95.

Transverse sections through the same embryo. Fig. 92, shows the abdominal plate, and Figs. 94, &95, the optic disc.

PLATE. 14

Figs. 96-97.

Longitudinal sections through the embryo seen in Fig. 93. Spores and sporulating cells now make their appearance.

Figs. 98-100.

Longitudinal, serial section through an embryo 6 hours older than that represented in Fig. 93, from the same prawn.

The stomodeum is beginning to form, as seen in the median section (Fig. 98, Std.)

The mesoderm is organized into a definite layer (Mes.), and the folds of the appendages are well developed.

Sporulating cells (S.C.) are very common.

PLATE. 15

Figs. 101 -106.

Five serial, longitudinal sections of early nauplius embryo. (12 hours older than last.) The abdominal fold is now being separated, by a transverse cleft in the ectoderm of the abdominal plate (A'.C.) Delaminating cells are seen in the optic disks, and spore formation is still prevalent.

Fig. 107.

Transverse section through optic disks, from similar egg.

Fig. 106

Longitudinal median section of embryo, older by several hours than the last, showing the abdominal cleft and fold, well developed.

The oesophagus is still a nearly straight tube (Std)

Fig. 108.

Longitudinal section from the same series as the last, to show the relations of the embryo to the egg, and also the distribution of the yolk cells.

PLATE 16

Fig. 109

Surface view of egg-nauplius.

Fig. 110. Surface view of a slightly older embryo, with 1-2 pairs of post mandibular appendages, which are concealed by the abdomen (Ab.).

Fig. 111

Egg-nauplius, greatly enlarged. A little less developed than the one in Fig 109., but from the same female.

Figs. 102, 103

Transverse and longitudinal median section of egg-nauplius of a small shore crab (possibly Sesarma), found at Beaufort, N. C

PLATE 17

Figs. 114-118.

Transverse, serial sections of the egg-nauplius. The plane of section is indicated by corresponding numbers in Fig. 113.

PLATE 18

Fig. 119-122.

Continuation of the series of Plate. 17., to illustrate the structure of the egg Nauplius.

PLATE. 19.

Fig. 123 124

Completion of series of transverse sections of egg nauplius, beginning Fig. 114 Plate. 17

Fig. 125.

Longitudinal section of the germ, in the plane, indicated in Fig. 111

Fig. 126.

Transverse section of an embryo a little younger than that shown in Fig. 106, in the region of the proctodaeum.

Fig. 127.

Transverse section of the egg-nauplius and egg, in the plane shown in Fig. 111.

Francis Hobart Herrick, the son of Rev. M. A. Herrick, D. D., and H. A. Putnam, was born in Woodstock, Vermont, Nov. 19. 1859. He received his early education at S. Paul's School, Concord, New Hampshire, and was graduated at Dartmouth College in 1881. He entered the Johns Hopkins University as a graduate student, and has spent four years in the study of Animal Morphology, his major subject, in the biological and marine laboratories of this University. His minor subjects were Animal Physiology and Vegetable Morphology.